

MORPHOLOGY, ADAPTATIONS,
AND RELATIONSHIPS OF
PLESIORYCTEROPUS, AND A
DIAGNOSIS OF A NEW ORDER OF
EUTHERIAN MAMMALS

R. D. E. MACPHEE

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First, . . . the animals were known only from disassociated scraps Second, [these] disassociated fragments . . . violated the Cuvierian "law" of association; it was impossible for a rational student to predict one part from another. Third, each part was decidedly *sui generis*, unlike anything else known. And fourth, in spite of that uniqueness, each part had certain (convergent, as we now know) broader similarities to various unrelated groups of mammals.

— G. G. Simpson (1970: 2), commenting on the systematic history of the South American marsupial family Argyrolagidae

ABSTRACT

Plesiorycteropus, an extinct mammal known only from the Quaternary of Madagascar, is conventionally regarded as a tubulidentate and therefore as closely related to extant *Orycteropus*. However, the shared derived traits that might support such an association have never been adequately identified or critically evaluated. The character analyses presented in this paper reveal that many of the identifiably derived traits of the skeleton of *Plesiorycteropus* are related to adaptations for digging. Aardvarks possess many of the same adaptations, but so do fossorial members of a broad diversity of other eutherian groups, including Dasypodidae, Manidae, Myrmecophagidae, Lipotyphla, and many others. Identifiably derived traits of *Plesiorycteropus* that have no obvious connection with digging are few, but the ones that can be adequately documented are by no means unique to aardvarks. Indeed, several of the apparently derived cranial and postcranial traits of *Plesiorycteropus* specifically echo conditions encountered in primitive ungulates, including various members of the paraphyletic assemblage Condylarthra. Accordingly, the view that *Plesiorycteropus* is unambiguously aardvarklike in its morphology and adaptations is not supported in this study.

To examine how a parsimony analysis of a stated character set might specify a placement for *Plesiorycteropus*, a 30-character, 16-taxon data matrix was formatted for the program Phylogenetic Analysis Using Parsimony. Two additional char-

acters, based on morphological assessments of key characters made by Bryan Patterson, were also used in some runs. Although the scale of morphological variation in *Plesiorycteropus* requires the recognition of two species, *P. madagascariensis* and *P. germainepetterae* n. sp., for the characters under consideration interspecific polymorphism was usually found to be negligible.

Although in most manipulations of the data matrix *Plesiorycteropus* tended to group with ungulates sensu lato (including Tubulidentata), its placement was unstable, and an exclusive sister-group pairing of *Plesiorycteropus* + Tubulidentata was rarely encountered. On the other hand, close pairings with xenarthrans, manids, and lipotyphlans did not occur unless the data matrix was purposely biased in those directions. As a minimum hypothesis, it may be concluded that *Plesiorycteropus* is apparently part of the great ungulate "bush," but a more exact placement is not convincingly provided by any of the cladistic solutions investigated. One resolution of this problem would be to refer *Plesiorycteropus* to superorder Ungulata as incertae sedis, but this would make it the only Recent mammal lacking a recognized ordinal affiliation. An alternative would be to consider *Plesiorycteropus* to be the sole known member of its own order. This is the resolution preferred here, on the ground that *Plesiorycteropus* is as morphologically distinctive as any eutherian group currently granted ordinal status. The new order **Bibymalagasiasia** is created for its reception.

INTRODUCTION

Plesiorycteropus, the sometime "Malagasy aardvark," may be justifiably described as the least familiar member of Madagascar's extinct Holocene fauna. Unlike giant lemurs and elephantbirds, *Plesiorycteropus* never excited much morphological or systematic in-

terest, having been the subject of only three detailed reports (Lamberton, 1946; Patterson, 1975; Thewissen, 1985) in the century since Filhol's (1895) original description. This inattention could be taken to imply that there is little to discuss—that *Plesiorycteropus* is

deemed to be so clearly a tubulidentate that additional treatments of its anatomy and relationships are unnecessary. The purpose of this monograph is to show that this assumption is seriously defective. Far from being an unquestionable aardvark affine, *Plesioryceropus* is not clearly referable to any named eutherian order, although it exhibits suggestive links to several. Analysis of these apparent linkages is crucial, because they may have implications for the higher-level systematics of a number of major groups. For these reasons, a thorough reinvestigation of *Plesioryceropus* is warranted.

This paper consists of three interdependent parts. The first part summarizes the taxonomic and systematic history of *Plesioryceropus*, showing how previous workers have come to very different conclusions about the phylogenetic position of this taxon. The second part is a detailed element-by-element anatomy of the skeleton of *Plesioryceropus*, with a focus on comparative and functional attributes. The last part, The Systematic Position of *Plesioryceropus*, uses the evidence critically evaluated in earlier sections to try to place *Plesioryceropus* on the eutherian cladogram. The results reported in this section illustrate how difficult it is to place, via parsimony treatments, isolated taxa that display many morphological novelties but few obvious synapomorphies linking them to other taxa. This problem can occur at any hierarchical level, but it is most prevalent in situations where higher taxa are being compared. This point has a certain obvious implication for the positioning of *Plesioryceropus*, and I have pursued it to what I consider to be its logical conclusion. Others will, of course, disagree with me, and I invite them to search for a different solution that does justice to all the facts.

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to specimens, and much useful information on the history of the collecting activities of the MNHN in Madagascar. I am also specially indebted to my colleague Darrel Frost, for long hours—and long arguments—spent on systematic philosophy and practice. Darrel Frost, Sherri McGehee, Malcolm McKenna, Michael Novacek, Kenneth Rose, and Hans Thewissen read and commented on various drafts of this paper. I am grateful for their counsel, some of which was actually followed. My greatest offering of thanks, however, is to Veronica MacPhee, for being an exacting reader, a hard debater, and a willing helper.

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Nearly all of the photographs and line drawings are the work of Lorraine Meeker, and nearly all of the labeling and much of the mounting was undertaken by Clare Fleming. Both Lorraine and Clare also prepared (or repaired) some of the specimens of *Plesioryceropus*, and I am indebted to both for the care they took in readying these materials for study. Chester Tarka contributed figures 38 and 39 (and much else in the way of advice) and Ed Heck drew figure 1. Audrone Bikenavicius (now at Ohio University) made the computations for the body weight estimates presented in table 14.

My paleontological fieldwork in Madagascar, conducted in cooperation with the Service de Paléontologie of the Oniversite ny Antananarivo, was made possible by grants from the National Geographic Society and National Science Foundation. I would especially like to thank Dr. Berthe Rakotosamimanana and Ernestine Raholimavo for their assistance, often under trying circumstances: *misaotra anareo indrindra, soava tsara!*

ABBREVIATIONS AND TOPONYMS

ABBREVIATIONS

Institutional

AM	Akademia Malagasy (Academie Malgache)
AMNHM	American Museum of Natural History, Department of Mammalogy
AMNHP	American Museum of Natural History, Department of Vertebrate Paleontology
MNHNA	Muséum National d'Histoire Naturelle, Laboratoire d'Anatomie Comparée, Paris
MNHNP	Muséum National d'Histoire Naturelle, Institut de Paléontologie, Paris
MHNHZN	Muséum National d'Histoire Naturelle, Laboratoire de Zoologie (Mammifères et Oiseaux), Paris
NHMLP	The Natural History Museum, London, Department of Palaeontology
OA	Oniversite ny Antananarivo (formerly Université de Madagascar, CUR Antananarivo)
PMU	Paleontologiska Museet, Upsala
USNMM	United States National Museum of Natural History, Division of Mammals
USNMP	United States National Museum of Natural History, Department of Paleobiology

Anatomical

(Initial letters of named muscles are capitalized in figures.)

a, aa	artery, arterial, arteries
acc	accessory
acetab	acetabulum
acous	acoustic
acrom	acromion
adds	adductores
adit	aditus
alisph	alisphenoid
ancon	anconeus
ant	anterior
apert	aperture(s)
artic	articular, articulation
ASP	alisphenoid bone
astrag	astragalus
aud	auditory
auric	auricular, auricularis
basiocc	basioccipital
basiot	basiotic
basisph	basisphenoid

bicip	bicipital
BOC	basioccipital bone
bord	border
br	brevis
brachial	brachialis
BSP	basisphenoid bone
Ca	caudal vertebra (with element number)
can	canal
canl	canaliculus
capit	capitulum
capsul	capsularis, capsule
car	carotid
carp	carpal, carpi
cart	cartilage
caud	caudal
cav	cavity
cnem	cnemial
coccyg	coccygeal
coch	cochlea, cochleae, cochlear
cond	condyle, condyloid
corac	coracoid
coron	coronoid, coronal
cotyl	cotyloid
cox	coxae, coxal
cr	crest, crista
cran	cranial
cranorb	cranio-orbital
crph	craniopharyngeal
cruc	cruciate
cyam	cyamella
delt	deltoid
deltpect	deltpectoral
dig	digital, digitorum
dipl	diploic
dist	distal
dors	dorsal
ect	ectal
ECT	ectotympanic bone
ectocr	ectocranial
ectoturb	ectoturbinal
ectotym	ectotympanic
emin	eminence
emiss	emissary
endocr	endocranial
endolym	endolymphatic
ENT	entotympanic bone
entepic	entepicondylar
entogl	entoglenoid
entotym	entotympanic
EOC	exoccipital bone
epicond	epicondyle
epitym	epitympanic
ETH	ethmoid bone
ethm	ethmoid
expans	expansion
ext	external

extens	extensor(es)	MAX	maxilla bone
fac	facet	MC	metacarpal
fem	femoris, femoral	meat	meatus, meatal
fen	fenestra(e)	med	medial, medius, medium, medialis
fib	fibula, fibular, fibularis	mening	meningeal
fis	fissure	metop	metopic
fl	flexor(es)	mid	middle
for	foramen (-mina)	min	minor
fos	fossa	MT	metatarsal
fov	fovea	n, nn	nerve, nerves
FRO	frontal bone	NAS	nasal bone
fron	frontal, fronto	navic	navicular
gastrocn	gastrocnemius	nonartic	nonarticular
gem	gemellus (-i)	nuch	nuchal
glas	glaserian	obsph	orbitosphenoid
glen	glenoid	OCC	occipital bone
glut	gluteal, gluteus	occip	occipital
gracil	gracilis	olecr	olecranon
grt	great, greater	ophth	ophthalmic
ham	hamulus	opt	optic
hamstr	hamstring	os	os, ossa
hd	head	OSP	orbitosphenoid bone
hypogl	hypoglossal	ov	ovale
iliopect	iliopectineal	palat	palatine
inc	incomplete	PAR	parietal bone
incud	incudis	paranas	paranasal
inf	inferior	paratym	paratympanic
infraorb	infraorbital	pariet	parietal, parieto
int	internal	parocc	paroccipital
intercond	intercondylar	pat	patellar
intermed	intermedius	pect	pectoralis
inteross	interosseous	pectin	pectineus
isch	ischial, ischiadic, ischium	percr	percranial
jug	jugular	peron	peroneus
JUG	jugal bone	perp	perpendicular
LAC	lacrimal bone	PET	petrosal bone
lacer	lacerate	petr	petrosal
lacr	lacrimal	pirif	piriform, piriformis
lam	lamina	pl	plate
lamb	lambdoidal	PMX	premaxilla bone
lat	lateral	poll	pollicis
latiss	latissimus	popl	popliteus
less	lesser	post	posterior
lig	ligament	posterolat	posterolateral
long	longus	posteromed	posteromedial
longit	longitudinal	postgl	postglenoid
Lu	lumbar vertebra (with element number)	postorb	postorbital
		postpalat	postpalatine
		posttym	posttympanic
lun	lunate	pr	process
m, mm	muscle, muscles	prim	primitivum
mag	magnum	prof	profundus
maj	major	prom	promontorium, promontory, promontorial
malleol	malleolus, malleolar		
mand	mandible	pron	pronator
marg	margin	prox	proximal
mast	mastoid	pseudogl	pseudoglenoid
max	maxillary		

pseudostyl	pseudostyloid
PSP	presphenoid bone
pt	part (of)
PTE	pterygoid bone
pteryg	pterygoid
quad	quadratus
rad	radius, radial, radialis
ram	ramus(-i)
rec	recess
rect	rectus
reg	region
retinac	retinaculum
rost	rostral
rot	rotundum
Sa	sacral vertebra (with element number)
sacr	sacral
sacrotub	sacrotuberous
sag	sagittal
sartor	sartorius
scap	scapula, scapular
scaph	scaphoid
sciat	sciatic
semilun	semilunar
semitend	semitendinosus
sept	septum
ses	sesamoid
sin	sinus
SOC	supraoccipital bone
sp	spine, spinous
sphen	sphenoid
sphenorb	spheno-orbital
sphenpal	sphenopalatine
sphenpet	sphenopetrosal
SQU	squamosal bone
squam	squamosal, squamoso-
stap	stapedial
styl	styloid
stylomast	stylomastoid
subarc	subarcuate
subopt	suboptic
subscap	subscapularis
sulc	sulcus
sup	superior
superf	superficial, superficialis
supin	supinator
suprameat	suprameatal
surf	surface
sust	sustentacular
sut	suture
tbl	tubal
teg	tegmen
temp	temporal, temporales
ten, tens	tendon, tendons
Th	thoracic vertebra (with element number)
tib	tibia, tibial, tibiale, tibialis
tr	transverse, transversarium

transarc	transarcual
trigem	trigeminal
triquet	triquetral
troch	trochanter, trochanteric
trochl	trochlea, trochlear
tub	tuberosity, tubercle
tym	tympanic, tympani
tymhy	tympanohyal
uln	ulnar
v, vv	vein, veins
vasc	vasculature, vessel(s)
vast	vastus
ven	venous
vent	ventral
vert	vertebra, vertebral
vest	vestibuli
vid	vidian (pterygoid)
zyg	zygomatic

Other

CI	consistency index (excluding uninformative characters, if applicable)
MPT	most parsimonious tree
ND	no data (element or morphological area missing or not measured)
RI	retention index
TL	tree length
UCI	nonambiguous character index
$\bar{X}$	arithmetic mean

TOPONYMS

In the text, current Malagasy orthography for place and institutional names is preferred over French equivalents (when different). However, locality names that are based on old Malagasy toponyms are retained in the interest of stability, even if the toponym is no longer in use (e.g., Ambolisatra, former place-name for a series of fossiliferous pond bottoms north of Toliary, in the area now known as Ambolomailaka). Lamberton frequently referred to localities by a combination of the name of the closest settlement (or other toponym) plus the name of the administrative district in which the settlement was located (e.g., Itasy Ampasambazimba, Tsi-rave Beroroha). In conformity with general practice I have dropped the vaguer name (usually the administrative district name) when referencing these sites. The concordance presented below should be consulted for unfamiliar cases.

Preferred	Former Name or Other Orthography
Anavoha	Beloha Anavoha
Ankevo	Ankavo
Antananarivo	Tananarive, Antananarive
Antsirabe	Sirabe, Sirabé
Belo	Belo-sur-mer
Masinandraina	Masinandreina
Sirave	Tsirave, Tsirave Beroroha
Toliary	Tuléar

SYNOPSIS OF *PLESIORYCTEROPUS* AND STATEMENT OF PROBLEM

INITIAL DISCOVERY

The systematic history of *Plesiorycteropus* begins with Filhol's (1895) naming of *P. madagascariensis* on the basis of a partial skull, found by the collector Grevé, at Belo in western Madagascar. The beginning was not propitious; Filhol's (1895: 14 [trans.]) account, meager and unillustrated, barely qualifies as a diagnosis even by the forgiving standards of 19th-century taxonomy:

Animal known from posterior portion of a skull, with closest affinities to *Orycteropus*. Same cranial sutures; same frontal sinus; same occipital condyles. Zygomatic arches stronger . . . Zygomatic process is stronger at its origin than is that of *Orycteropus*, which requires that we present our determination with reservations.

Although Grevé found numerous remains of extinct lemurs and other vertebrates at Belo in addition to the type skull (now MNHNP 328; see table 1), there is no record of his finding additional specimens referable to *Plesiorycteropus*, and Filhol (1895) certainly did not describe any. For the next fifty years, commentators could do little more than repeat, on Filhol's authority, that a possible aardvark relative had been found in a Quaternary locality in coastal western Madagascar (e.g., Weber, 1904, 1928; Ameghino, 1905; G. Grandidier, 1905; Winge, 1915). Sonntag and co-workers failed to mention *Plesiorycteropus* at all in their otherwise comprehensive papers on aardvark morphology and evolution (Sonntag, 1925; Sonntag and Woollard, 1925; Le Gros Clark and Sonntag, 1926). Colbert (1933) referred to *Plesiorycteropus* only to make the point that aardvarks reached Madagascar in the Pleistocene (!), evidently on the assumption that the Malagasy

subfossil hardly differed from extant *Orycteropus*.

LAMBERTON: THE EDENTATE HYPOTHESIS

The next landmark in the systematic history of *Plesiorycteropus* was the publication, in 1946,¹ of a detailed study by the eminent French paleontologist Charles Lambertson. Lambertson spent his entire scientific career working on the Quaternary fauna of Madagascar, and his collected works were then, and remain today, important sources of information on the recently extinct animals of the island. During the 1920s and 1930s, as opportunity offered, Lambertson excavated a number of subfossil sites in central and southern Madagascar (Lamberton, 1934, 1948). Among the fossils recovered at these sites were some highly unusual specimens that were difficult to place systematically (Lamberton, 1930). At first he assumed that they represented the form named *Hypogeomys boulei* by G. Grandidier (1912), an alleged giant nesomyine rodent (see Material, Taxonomy, and Occurrence). However, he quickly acknowledged that morphological departures from rodents were so great that some other allocation was indicated. The only plausible one was Filhol's obscure *Plesiorycteropus madagascariensis*.

Lamberton is sometimes cited in the secondary literature as having demonstrated, or at least as having accepted for lack of a better alternative, the tubulidentate affinities of *Plesiorycteropus* (e.g., Chanudet, 1975). This is close to a misrepresentation. The fact is that Lambertson avoided making any settled allocation, because he was frankly bewildered by the emphatic resemblances that *Plesiorycteropus* displayed in some features to aard-

¹ This paper is sometimes cited as "Lamberton (1942-43)," which corresponds to the *annuaire* date of the *Bulletin de l'Académie Malgache* in which it was published, but not to the date of submission (October 1944) or publication (1946). The Akademia Malagasy suspended its scientific series during the British occupation of Madagascar in World War II, and the *annuaire* for 1942-43 was not finally printed until 1946, the date on the first interior title page. Its illustrations are far below the quality seen in Lambertson's other monographs, possibly because of postwar shortages of materials.

varks, in others to pangolins, and in still others to armadillos and vermilings. In the end he offered three alternative hypotheses (Lamberton, 1946: 48–49; see also Lamberton, 1948): (1) *Plesiorcyteropus* is a paleontological chimaera, its hypodigm being composed of parts of several quite different mammals; (2) the hypodigm of *Plesiorcyteropus* represents only a single kind of mammal, but one diversely convergent on a variety of unrelated taxa and therefore of very uncertain affinity; or (3) *Plesiorcyteropus* had an *organisation synthétique*, combining in one form ancestral traits that have been lost in various derivative lineages. Although in several passages in his 1946 paper he admitted to some lingering doubts about the unity of the hypodigm of *Plesiorcyteropus* as he had assembled it, he did not think that the first hypothesis was the most probable of the three. With respect to the second, he noted in the summary at the end of his paper that *Plesiorcyteropus* displayed the greatest number of resemblances to aardvarks, but immediately went on to list a series of features in which it was strikingly different from tubulidentates. In view of these ambiguities and the not-incidental point that there are no teeth ascribable to this taxon (see below), Lamberton felt compelled to conclude that unequivocal attribution of *Plesiorcyteropus* to Tubulidentata was not then possible.

The third hypothesis offered a different sort of solution, one which Lamberton (1946) developed in some detail. Suppose, he argued, that *Plesiorcyteropus* was a member of a lineage whose separate ancestry stretched far back into the Tertiary. Suppose also that the odd mix of traits exhibited by *Plesiorcyteropus* was present in the basal ancestors of certain other, related eutherian groups. The lineage that culminated in Quaternary *Plesiorcyteropus*, living on an island *confiné et tranquille*, evolved very slowly and retained its primitive aspect. The other groups, presumably under more intense selection pressures, became so modified in the course of their evolution that the primitive traits characteristic of their joint early ancestor(s) were mostly lost or otherwise extensively modified.

For Lamberton, the “other groups” to which *Plesiorcyteropus* was related were the edentates—not the edentates of some recent,

phylogenetic classifications of Mammalia (e.g., Novacek, 1986), but instead the older, Cuvierian concept that brigaded xenarthrans, tubulidentates and pholidotans into a single taxonomic unit. This assemblage was thoroughly unfashionable by 1946, and it is peculiar that Lamberton did not consider any of the long-available arguments (e.g., Gregory, 1910; Weber, 1891, 1928) against including tubulidentates and pholidotans within *Edentata,² old style. Nevertheless, the possibility that *Plesiorcyteropus* was an *Ur-edentate* was clearly attractive to him. In his text he consistently referred to the Malagasy fossil as an *édenté*, and in his only really concrete statement on the affinities of *Plesiorcyteropus*, he claimed that the bones of this animal appeared “beyond any doubt” to belong “to some animal of the Edentata group” (Lamberton, 1946: 49 [his English summary]). In this connection it is retrospectively interesting that Lamberton did not discuss or even refer to a possible link between *Plesiorcyteropus* and the primitive ungulates then widely and still commonly referred to as condylarthrans. Evidence for and against a relationship between aardvarks and ungulates had been incidentally discussed by Lönnberg (1906), Gregory (1910), Jepsen (1932), and Colbert (1941), and was reviewed at considerable length by Le Gros Clark and Sonntag (1926). Although Lamberton (1946) referenced the three last-cited papers in his bibliography, he did not pursue their conclusions with respect to tubulidentate relationships in general or those of *Plesiorcyteropus* in particular.

If nothing else, Lamberton’s (1946) tentative analysis of *Plesiorcyteropus* should have kindled debate in edentate historical biogeography of the sort that engulfed Ameghino’s (1905) discussion of this topic a generation earlier. However, Lamberton’s monograph appears to have been widely ignored and, except for a smattering of later references, *Plesiorcyteropus* fell back into obscurity. A decade later, MacInnes (1956) briefly compared the limb bones of *Plesiorcyteropus* to those of *Myorycteropus africanus*, a Miocene aard-

² Throughout the text, asterisks are placed in front of names of certain supraspecific taxa that are not admitted to be monophyletic. For further explanation, see p. 26.

vark from Rusinga Island. Although he tacitly accepted *Plesiorycteropus* as a tubulidentate, he noted many differences in limb anatomy and concluded that the relationship between the Malagasy and Rusingan taxa could not be very close. Lavocat (1958) accepted *Plesiorycteropus* as a tubulidentate, but like Lamberton expressed lingering reservations about its placement. But in the main, *Plesiorycteropus* was simply not a player in anyone's systematic scenario; it did not, for example, rate even a casual mention in Darlington's (1957) discussion of the zoogeographical connections of Madagascar.

PATTERSON:

THE TUBULIDENTATE HYPOTHESIS

HOMOLOGY, ADAPTATION, AND CONVERGENCE

In the 1970s, Bryan Patterson took up the study of *Plesiorycteropus* as one component of his revision (Patterson, 1975) of all fossil tubulidentates then known. Like Lamberton, he concluded that the hypodigm of *Plesiorycteropus* consisted of only one type of animal. Unlike Lamberton, he concluded that the evidence permitted no doubt about its systematic position. In Patterson's (1975) view, the issue of the near affinities of *Plesiorycteropus* among living mammals could be restricted to consideration of two groups, Tubulidentata and Pholidota. Unsurprisingly, he considered the supposed edentate traits of *Plesiorycteropus* as identified by Lamberton to be the result of multiple convergences among quite unrelated taxa, and therefore of no particular systematic moment. Xenarthrans as such are scarcely mentioned in his text, and it is clear that he considered any comparisons with this group to be worthless except where function was concerned. Having disposed of any possible edentate connection to his satisfaction, he went on to develop his principal conclusions, that *Plesiorycteropus* was unquestionably a tubulidentate, and that tubulidentates were ultimately derived from some source within *Condylarthra. So persuasive was he that his major conclusions about the phylogeny of aardvarks have been adopted by most later authors without reservation (but see following section and Thewissen [1985]).

In conformity with widespread practice at the time, Patterson (1975, 1978) did not sharply or consistently discriminate between plesiomorphies and apomorphies, nor did he provide specific character analyses for the purpose of demonstrating that *Plesiorycteropus* was a member of a demonstrably monophyletic Tubulidentata. Instead, he utilized the vaguer standards of the eclectic or "evolutionary" paradigm (e.g., Simpson, 1975), in which relationships are stipulated according to the researcher's sense of the balance of probabilities, as provided by morphological indicators, adaptive scenarios, biogeographical hypotheses, and geological age. There was and is nothing objectionable about using such devices to frame phylogenetic questions: like finding a trout in the milk, circumstantial evidence can be very strong (Thoreau, 1854). However, it is important to provide some meaningful tests of ensuing results, without which the eclectic approach (like any other) may mislead as much as it leads. The following example of Patterson's procedures is instructive in this regard.

In developing his edentate hypothesis, Lamberton (1946) made much of the fact that *Plesiorycteropus* displayed numerous resemblances to manids. While Patterson freely admitted that *Plesiorycteropus* possessed several unusual features quite unknown outside Pholidota, he nevertheless preferred to conclude that "resemblances between *Plesiorycteropus* and the manids in skull structure are adaptive in nature, and hence convergent; those between it and the orycteropodines are indicative of affinity" (Patterson, 1975: 213). In Patterson's estimation, the outstanding adaptive resemblance that *Plesiorycteropus* displayed to manids was edentulousness, a trait which he inferred from negative evidence. Most extinct Malagasy mammals are richly represented by dental fossils, but no teeth or jaws distinctive of aardvarks (or indeed any other "unknown" mammal) have ever shown up in Quaternary sites. This leaves only two possibilities for *Plesiorycteropus*: either its teeth were profoundly and inseparably convergent on those of some other group—and none suggests itself—or it had no teeth at all. Patterson (1975) preferred the second alternative, and proposed that *Plesiorycteropus* was a fully committed myrmecophage

TABLE 1
Catalog of Identified Specimens of *Plesiorycteropus*

	Element ^a	Locality	Notes ^b
Muséum National d'Histoire Naturelle, Institut de Paléontologie (MNHN)			
327 ^c	cranium	Ampasambazimba(?)	# Lambertson (1946); (H) <i>P. germainepetterae</i>
328	cranium	Belo	# Filhol (1895); † 1906-17; (H) <i>P. madagascariensis</i>
329	femur	—	ref. <i>P. germainepetterae</i>
330	ulna	Ambolisatra	† 1905-8
331	humerus	—	
332	tibiofibula	Sirave	§ "Tsirave 1931"
333	radius	—	
334	femur	—	
335	tibiofibula	—	
336/340	tibiofibula	—	
337	tibiofibula	Anavoha	§ "Beloha Anavoha 1932"
338	femur	Sirave	§ "Tsirave 1931"
339	innominate	—	
341	femur	—	
342	femur	Antsirabe	§ "Antsirabe"
343	femur	Sirave	§ "Tsirave 1931"
344	femur	Sirave	§ "Tsirave Beroroha"
345	femur	Sirave	§ "Tsirave 1931"
346	innominate	—	
347	humerus	—	
348	femur	—	
361	innominate	—	
513	caudal	?Ankevo	† 1910-33
515	lumbar	?Ankevo	† 1910-33
534	cranium	Ambolisatra	# Lambertson (1946); † 1905-8; ref. <i>P. madagascariensis</i>
540	lumbar	Ambolisatra	# Lambertson (1946); † 1905-8; ref. <i>P. madagascariensis</i>
541	lumbar	Ambolisatra	# Lambertson (1946); † 1905-8; ref. <i>P. madagascariensis</i>
542	lumbar	Ambolisatra	# Lambertson (1946); † 1905-8; ref. <i>P. madagascariensis</i>
543	lumbar	Ambolisatra	# Lambertson (1946); † 1905-8; ref. <i>P. madagascariensis</i>
1650	caudal	—	
1651	caudal	—	
1652	caudal	—	
1653	caudal	—	
1654	astragalus	Ampasambazimba	# Lambertson (1946)
1655	astragalus	Sirave	# Lambertson (1946)
1656	metapodial ?V or ?I	Sirave	# Lambertson (1946)
1657	metapodial II	Sirave	# Lambertson (1946)

TABLE 1—(Continued)

	Element ^a	Locality	Notes ^b
1714	caudal	Ambolisatra	† 1905-8; ref. <i>P. madagascariensis</i>
1715	caudal	Ambolisatra	† 1905-8; ref. <i>P. madagascariensis</i>
1716	caudal	Ambolisatra	† 1905-8; ref. <i>P. madagascariensis</i>
1717	caudal	Ambolisatra	† 1905-8; ref. <i>P. madagascariensis</i>
1718	caudal	Ambolisatra	† 1905-8; ref. <i>P. madagascariensis</i>
Muséum National d'Histoire Naturelle, Laboratoire d'Anatomie Comparée (MNHNA)			
1987.030	innominate	Ampoza	§ "Village Ampoza"
1987.031	humerus	—	§ "Collection Grandidier" ^d
1987.032	radius	—	§ "Collection Grandidier"
1987.033	ulna	—	§ "Collection Grandidier"
1987.034	scapula	Ampoza	§ "Village Ampoza"
1987.035	humerus	Ampoza	§ "Village Ampoza"
1987.036	humerus	Ampoza	§ "Village Ampoza"
1987.037	femur	Ampoza	§ "Village Ampoza"
1987.038 ^c	femur	Ampasambazimba	# Grandidier (1912); ref. <i>P. madagascariensis</i>
1987.039	ulna	—	§ "Collection Grandidier"
1987.040	femur	Ampoza	§ "Village Ampoza"
1987.041	tibiofibula	Ampoza	§ "Village Ampoza"
1987.042	tibiofibula	Ampoza	§ "Village Ampoza"
1987.043A	atlas	Antsirabe	# Lamberton (1946)
1987.043C ^f	thoracic	Ampoza	§ "Village Ampoza"
1987.043D	thoracic	Ampoza	§ "Village Ampoza"
1987.043E	thoracic	Ampoza	§ "Village Ampoza"
1987.043F	thoracic	—	
1987.043G	thoracic	—	
1987.043H	thoracic	—	
1987.043J	thoracic	Ampoza	§ "Village Ampoza"
1987.043K	lumbar	Ampoza	§ "Village Ampoza"
1987.043L	lumbar	Ampoza	§ "Village Ampoza"
1987.043M	lumbar	Ampoza	§ "Village Ampoza"
1987.043N	sacrum	Ampoza	§ "Village Ampoza"
1987.043O	caudal	Ampoza	§ "Village Ampoza"
1987.043P	caudal	Ampoza	§ "Village Ampoza"
1987.043Q	caudal	Ampoza	§ "Village Ampoza"
1987.043R	caudal	Ampoza	§ "Village Ampoza"
1987.043S	caudal	Ampoza	§ "Village Ampoza"
1987.043T	caudal	Ampoza	§ "Village Ampoza"
1987.043U	caudal	Ampoza	§ "Village Ampoza"
1987.044A	astragalus	Sirave	# Lamberton (1946)

TABLE 1—(Continued)

	Element ^a	Locality	Notes ^b
1987.044B	astragalus	Ampoza	§ "Village Ampoza"
1987.044C	metapodial IV	Sirave	# Lamberton (1946)
1987.044D	metapodial IV	Sirave	# Lamberton (1946)
1987.044E	metapodial II	Sirave	# Lamberton (1946)
1987.044F	metapodial ?II or ?IV	Ampoza	§ "Village Ampoza"
1987.044G	intermediate phalanx	Sirave	# Lamberton (1946)
1987.044H	proximal phalanx	Sirave	# Lamberton (1946)
1987.044J	distal phalanx	Sirave	# Lamberton (1946)
1987.044K	distal phalanx	Sirave	# Lamberton (1946)
Natural History Museum, London, Department of Palaeontology (NHMLP)			
M 7082	humerus	Antsirabe	§ "marshes of Sirabé"
M 7085 ^c	innominate	Antsirabe	# Forsyth Major (1908); ref. <i>P. madagascariensis</i>
M 9946	tibiofibula	—	# Carleton (1936)
Unnumbered	femur	—	
Unnumbered	innominate	—	
Paleontologiska Museet, Upsala (PMU)			
M 5095	innominate	Masinandraina	# Ekblom (1953); § "Masinandreina"
Akademia Malagasy (AM) ^d			
Unnumbered	femur	Ampasambazimba	§ "Itasy, Ampasambazimba, 1913"
Unnumbered	femur	Bemafandry	§ "Bemafandry"
Unnumbered	femur	Antsirabe	§ "Antsirabe"
Unnumbered	femur	Antsirabe	§ "Antsirabe"
Unnumbered	femur	Antsirabe	§ "Antsirabe"
Unnumbered	femur	Antsirabe	§ "Antsirabe"
United States National Museum of Natural History, Division of Paleobiology (USNMP)			
474080	cranium	Anjohibe	# Burney et al., in press; ref. <i>P. madagascariensis</i>
474081	radius	Anjohibe	# Burney et al., in press
474082	tibiofibula	Anjohibe	# Burney et al., in press
474083	metapodial ?V or ?I	Anjohibe	# Burney et al., in press
474084	proximal phalanx	Anjohibe	# Burney et al., in press
Rejected specimens ^e			
MNHNP 1658			
MNHNP 1719	proximal phalanx	Sirave	# Lamberton (1946)
MNHNA	clavicle	?Ankevo	† 1910-33
1987.043B	cervical	Ampoza	§ "Village Ampoza"

^a Some MNHNP collections have been given new alphanumeric accession strings in recent years; the new strings for Madagascar include the designator “MAD,” which should be understood in all text references (e.g., MNHNP 327 is properly MNHNP MAD 327). In the present table, older accession numbers (year of accession + sequence number) are also provided and used as a basis for determining locality, as follows: 1905-8, museum expedition under Geay (Ambolisatra); 1906-17, gift of G. Grandidier (specimens found by Grevé and Grandidier in the “marais et grottes de Madagascar,” probably mostly from Ambolisatra); and 1910-33, gift of Barfèty and Bühner (specimens from “cercle de Morondava,” assumed to mean Ankevo, a site they are known to have excavated [Chanudet, 1975]).

^b Key: (H), holotype; ref., referred to. Locality based on illustrations or other identifying information in reference noted (#), MNHNP catalog entry (†), or information accompanying or written on specimens (§). Site designations can be very vague; Lamberton’s “Antsirabe” locality is very unlikely to be precisely the same as the one excavated by Forsyth Major, for example.

^c The only locality designation for MNHNP 327 is “centre d’île,” which in Lamberton’s publications usually meant (and is assumed here to mean) Ampasambazimba.

^d In MNHNA collections, “Collection Grandidier” is a general designator for gifts made to this institute by G. Grandidier. Exact localities are not provided.

^e Holotype of *Hypogeomys boulei* (G. Grandidier, 1912).

^f The thoracics labeled MNHNA 1987.043C-E and 1987.043K were contained in a box marked “Village Ampoza”; MNHNA 1987.043F-H were located in another, unmarked box. They may or may not be part of the set of five thoracics from Antsirabe described by Lamberton (1946).

^g Holotype of *Majoria* [= *Myoryctes*] *rapeto* (Forsyth Major, 1908; Thomas, 1915 [replacement name]).

^h The collection of Akademia Malagasy (AM), consisting exclusively of femora, is currently in the safekeeping of the Service de Paléontologie, OA.

ⁱ Rejected specimens: specimens included with *Plesiorycteropus* collections of MNHNP and MNHNA, but probably belonging to lemurs.

on the model of pangolins and vermilings, having followed the alleged "trend" toward tooth reduction in orycteropodids to its ultimate end.³

This explanation is, of course, a typical evocation of a typical convergence argument, and it is acceptable as far as it goes. To buttress his adaptational argument further, however, Patterson entertained a still more profound convergence between *Manis* and *Plesiorycteropus*: not only was *Plesiorycteropus* edentulous, it had also convergently developed a manidlike jaw articulation, whereby the much-reduced mandible articulates with a tiny mandibular fossa perched on the underside of the zygomatic process of the squamosal. He allowed that this was a point of major contrast with aardvarks, but did not go on to mention that pholidotan jaw joints are unique in the respects just listed: not even myrmecophagids have isolated the entire craniomandibular joint on a process of the squamosal. (As it happens, Patterson's identification of the position of the craniomandibular joint in *Plesiorycteropus* is incorrect [see Morphology of the Cranium]: it is certainly not manidlike, but it is not aardvark-like either.)

At this point the reader is forced to ask why this last feature must be interpreted as a convergence, when it could be just as parsimoniously explained as a decisive synapomorphy supporting a sister-group relationship between *Plesiorycteropus* and Pholidota. The answer, of course, is that Patterson didn't employ parsimony as an aid for phylogenetic inference: *Plesiorycteropus* was an aardvark, and any resemblances of a specialized sort to nonaardvarks were to be regarded as accidents of evolutionary design. Whether or not one agrees with the methodology he used to arrive at this conclusion, is it nevertheless a valid inference from the information Patterson had available?

A CONSISTENCY TEST OF THE TUBULIDENTATE HYPOTHESIS

This section examines the character support for Patterson's version of the tubulidentate hypothesis, viz. that *Plesiorycteropus* + Orycteropodidae form a monophyletic unit, related in some unspecified way to some or all *Condylarthra. The point of interest here is to ascertain whether Patterson's (1975, 1978) own data support his hypothesis regarding the placement of *Plesiorycteropus* as strongly as he implied.

From Patterson's (1975, 1978) papers, I extracted 41 character states of *Plesiorycteropus* that were defined with sufficient explicitness to permit characterization. These are set out in table 2 in the form of a concordance, in which conditions in *Plesiorycteropus* are rated alongside those found in condylarthrans, orycteropodids, manids, dasypodids, and tenrecids. Boldface entries are based as far as possible on Patterson's (1975, 1978) actual statements, although some textual deconstruction was necessary to interpret his apparent intent in certain cases. These entries may be said to represent the minimum data set that Patterson explicitly used in coming to his systematic conclusions. However, Patterson was rarely explicit about all of the comparisons that had to be made. Entries in regular type are my assessments, based on what I believe Patterson knew (or should have known) about character distributions. Where Patterson's assessment is available I have made none of my own, even though in certain cases I would have defined character distributions rather differently. The following points should be borne in mind while examining this table:

(1) Patterson's comparisons involving *Plesiorycteropus* were essentially limited to three groups: orycteropodids (*Orycteropus*, *Myorycteropus*, and *Leptorycteropus*, organized by him as subfamily Orycteropodinae), pholidotans (extant *Manis* only), and condylarthrans. In the case of the last, his direct comparisons were few and largely limited to observing that one or another trait of some member of Orycteropodidae can be found in one or another condylarthran genus (usually, one or more of *Hyopsodus*, *Ectoconus*, *Arcotocyon*, *Phenacodus*, and *Meniscotherium*).

³ Interestingly, Lamberton (1946: 27) believed exactly the reverse—that *Plesiorycteropus* probably had a dentition better developed than in most other members of *Edentata. Since the sloping occipital nuchal planum of vermilings and pangolins was correlated with reduction of the anterior dentition, he argued, the vertical planum of the Malagasy subfossil must signify nonreduction.

As traditionally conceived, *Condylarthra is about as obviously a paraphyletic group as may be found in Mammalia (Thewissen and Domning, 1992), and, treated as a terminal taxon, its character analysis is highly ambiguous (as indicated by the number of polymorph entries under this heading).

(2) Patterson (1975, 1978) made virtually no explicit comparisons to dasypodids and none at all to tenrecids; these taxa have been included to place character distributions in a broader perspective. Inclusion of dasypodids in the comparisons is justified by his attack on Lamberton's edentate hypothesis, while tenrecids, as primitive Malagasy eutherians, offer a convenient outgroup.

(3) In table 2, wherever a compared taxon exhibits a close similarity to *Plesiorcyteropus*, I have designated the relevant character state **as in P** (indicating assessment is Patterson's) or *as in P* (indicating assessment is mine). This convention requires some explanation. As earlier noted, Patterson (1975) argued that any important similarities between *Plesiorcyteropus* and pholidotans or dasypodids could be dismissed as homoplasies, while those jointly exhibited by *Plesiorcyteropus* and aardvarks (and condylarthrans in some instances) were always "indicative of affinity," i.e., homologously shared. In context he was presumably largely focussing on what we would now categorize as derived traits. However, because he provides no textual basis for discriminating between primitive and derived traits, I do not attempt to do so in the table. Obviously, were I to have merely accepted Patterson's prescription concerning homologies and convergences among the groups compared, there would be no point in undertaking the present assessment. It is therefore important to reiterate that table 2 does not represent Patterson's viewpoint exclusively, but is a necessary hybrid of his published comments and my interpretations.

None of the foregoing is intended to disparage Patterson's (1975, 1978) papers, which are models of expository writing within an eclectic framework. However, these points do underscore that any effort to extract unequivocal trait distributions and polarity evaluations from evidentiary presentations not designed for that purpose requires considerable extrapolation and infilling of missing data.

To simplify the assessment of character distributions, I have reduced the Patterson character states (PCS) expressed in table 2 to binary code in table 3 (1 = match, or 0 = no match with character state in *Plesiorcyteropus*; 0,1 = terminal taxon is polymorphic). In table 3, matches are further subdivided into ones explicitly identified by Patterson (encircled 1s) and ones that were not (bold-face 1s). "Matches" are here understood to mean phenotypic resemblances, whether due to convergence or to homology.

If we disregard Patterson's aprioristic conclusions about homology cited at the end of the previous section, then the following conclusions are warranted:

(1) If attention is restricted to Patterson's explicit matches, out of 41 potential pairings *Plesiorcyteropus* resembles *Condylarthra in 17 instances (polymorphics included), Orycteropodidae in 19, Manidae in 8, and Dasypodidae in only 2.

(2) Fourteen states are jointly shared by *Plesiorcyteropus*, *Condylarthra, and Orycteropodidae. Of these, 4 are also found in manids; none occurs in dasypodids or tenrecids. This leaves 10 character states as potentially "exclusive" resemblances of *Condylarthra + Orycteropodidae + *Plesiorcyteropus*.

These results seem clear enough in terms of their systematic implications, but there are several problems with their acceptability, even when viewed within the context of the eclectic paradigm. First, it is obvious that Patterson was rather tendentious in his comparisons. For example, what inference may be drawn from the lack of stated similarities to Dasypodidae when only two explicit comparisons (character states 33 and 36, both positive) involving this family and *Plesiorcyteropus* were made? Secondly, Patterson defined some character states ambiguously, leaving the reader uncertain about their distribution. For example, it is not clear to me how Patterson evaluated the character state "greatly reduced dentition" for Orycteropodidae (PCS 2). In fact his remarks can be taken in different ways: *Leptorycteropus* is offered (Patterson, 1975: 228) as an example of a primitive tubulidentate with a complete eutherian tooth formula, implying that the reduction in anterior loci seen in *Orycteropus*

TABLE 2
Character States of *Plesiorhycteropus* According to Patterson (1975), Compared to States in Some Other Mammals (I)

Character state in <i>Plesiorhycteropus</i> ^a	*Condylarthra	Orycteropodidae	Manidae	Dasyrodidae	Tenrecidae
*1. Mandibular fossa restricted to zygomatic process	not restricted	not restricted	as in <i>P</i>	not restricted	not restricted
*2. Teeth greatly reduced or absent	unreduced	[<i>polymorph</i>] ^b	as in <i>P</i>	as in <i>P</i>	unreduced
*3. Zygomatic arch interrupted	uninterrupted	uninterrupted	as in <i>P</i>	uninterrupted	as in <i>P</i>
4. Alisphenoid epitympanic wing large ^c	as in <i>P</i>	as in <i>P</i>	as in <i>P</i>	small	as in <i>P</i>
5. Preotic crest	as in <i>P</i>	as in <i>P</i>	absent	as in <i>P</i>	as in <i>P</i>
6. Epitympanic sinus absent	[<i>polymorph</i>] ^d	large	large	as in <i>P</i>	as in <i>P</i>
7. Petrosal not inclined	as in <i>P</i>	vertical	as in <i>P</i>	as in <i>P</i>	as in <i>P</i>
8. Mastoid region dorsally well exposed	[<i>polymorph</i>]	as in <i>P</i>	not exposed	little exposed	as in <i>P</i>
9. Facial portion of lacrimal large	as in <i>P</i>	as in <i>P</i>	small or nonexistent	as in <i>P</i>	small
10. Lacrimal foramen intraorbital or marginal	as in <i>P</i>	extraorbital	extraorbital	[<i>polymorph</i>] ^e	as in <i>P</i>
11. Parietal-alisphenoid contact absent	present	present	as in <i>P</i>	[<i>polymorph</i>] ^f	present
12. Orbitosphenoid large	[?]	as in <i>P</i>	small	small	small
13. Postorbital process absent	[<i>polymorph</i>]	present	as in <i>P</i>	as in <i>P</i>	as in <i>P</i>
14. Postglenoid foramen present	as in <i>P</i>	absent	as in <i>P</i>	as in <i>P</i>	as in <i>P</i>
15. Alisphenoid canal absent	[<i>polymorph</i>]	as in <i>P</i>	as in <i>P</i>	as in <i>P</i>	present
16. Rostral widening of nasals present	absent	absent	absent	[<i>polymorph</i>] ^g	absent
17. Occipital vertical	as in <i>P</i>	[<i>polymorph</i>] ^h	acute	as in <i>P</i>	as in <i>P</i>
18. Paroccipital process small or absent	as in <i>P</i>	as in <i>P</i>	as in <i>P</i>	as in <i>P</i>	large
19. Marked caudad increase in size of thoracics and lumbaris	[<i>polymorph</i>] ⁱ	as in <i>P</i>	minor	minor	minor
20. Sacrum caudally enlarged	not enlarged	as in <i>P</i>	increase	increase	increase
21. Xenarthrous articulations absent	as in <i>P</i>	as in <i>P</i>	as in <i>P</i>	as in <i>P</i>	not enlarged
22. Deltpectoral area projects laterally	as in <i>P</i>	as in <i>P</i>	projects ventrally	as in <i>P</i>	as in <i>P</i>
23. Supinator crest moderate	[<i>polymorph</i>]	prominent	prominent	prominent	as in <i>P</i>
24. Medial epicondyle of humerus not proximodistally expanded	as in <i>P</i>	as in <i>P</i>	expanded	as in <i>P</i>	as in <i>P</i>
25. Distal articular surface of ulna small	large	large	large	large	as in <i>P</i>
26. Shaft of radius greatly compressed (flattened)	not greatly compressed	not greatly compressed	as in <i>P</i>	as in <i>P</i>	not greatly compressed
27. Bicipital tuberosity indistinct	distinct	distinct	as in <i>P</i>	as in <i>P</i>	distinct
28. Lateral process of ischium present	absent	as in <i>P</i>	absent	absent	absent
29. Ischium does not extend caudal to ischial tuberosity	as in <i>P</i>	extends caudally	as in <i>P</i>	as in <i>P</i>	as in <i>P</i>

TABLE 2—(Continued)

Character state in <i>Plesiorhycteropus</i> ^a	*Condylarthra	Orycteropodidae	Manidae	Dasypodidae	Tenrecidae
30. Iliosacral articulation rostral to rectus tubercle	medial	medial	medial	as in <i>P</i>	as in <i>P</i>
31. Ilium not expanded caudodorsally	expanded	[<i>polymorph</i>]	as in <i>P</i>	as in <i>P</i>	as in <i>P</i>
32. Rectus and iliopectineal tubercles prominent	as in <i>P</i>	as in <i>P</i>	rectus only	as in <i>P</i>	as in <i>P</i>
33. Greater trochanter projecting above femoral head	[<i>polymorph</i>]	not projecting	not projecting	as in <i>P</i>	not projecting
34. Lesser trochanter large, medially projecting	[<i>polymorph</i>]	small, not projecting	as in <i>P</i>	as in <i>P</i>	as in <i>P</i>
35. Patellar groove shallow	deep	deep	as in <i>P</i>	as in <i>P</i>	deep
36. Tibia and fibula fused proximally and distally	neither fused	neither fused/	neither fused	as in <i>P</i>	neither fused ^k
37. Distal articular surface of tibia anteroposteriorly compressed	not	not	not	as in <i>P</i>	not
38. Tibia bowed, with interosseous crest	compressed	compressed	compressed	as in <i>P</i>	compressed
39. Astragalar trochlea shallow	[<i>polymorph</i>]	[<i>polymorph</i>]	not bowed	as in <i>P</i>	not bowed
40. Facet on astragalus for medial malleolus of tibia	deep	deep	as in <i>P</i>	as in <i>P</i>	deep
41. Astragalar foramen absent	[<i>polymorph</i>] ^j	as in <i>P</i>	absent	absent	absent
		present	as in <i>P</i>	as in <i>P</i>	as in <i>P</i>

^a In first column, character states for *Plesiorhycteropus* are as defined by Patterson (1975). Character states for other taxa are coded as follows: boldface entries are based on Patterson's (1975) evaluation; entries in regular type are based on my evaluation. As in *P* (or as in *P*) means that structure is considered the same in *Plesiorhycteropus* and compared taxon. **Polymorph** (or *polymorph*) means that more than one state exists within taxon for character under consideration. Contents of *Condylarthra are not defined by Patterson; conditions reported in table are primarily based on *Arctocyon*, *Hyopsodus*, *Meniscotherium*, and *Phenacodus*. Character states 1–3 for *Plesiorhycteropus* (asterisks) are inferential; see text.

^b Coded as polymorphic because Patterson (1975) made a special point of the fact that *Leptorycteropus* had the normal eutherian cheek tooth number.

^c I would not rate epitympanic wing of alisphenoid in *Plesiorhycteropus* as "large," but have followed Patterson's explicit statement.

^d The traditional view, followed by Patterson, is that condylarths lack epitympanic sinuses. However, Cifelli (1982) described a posterior petrosal epitympanic sinus for *Phenacodus* and *Meniscotherium*.

^e Extraorbital in *Dasypus*.

^f Usually absent, but present in *Tolypeutes*.

^g Widening present in many dasypodids.

^h *O. gaudryi* has a vertical occiput.

ⁱ Increasing vertebral dimensions in condylarths recorded only for *Meniscotherium* (Gazin, 1965).

^j Only fused proximally in *Orycteropus*.

^k Tibia and fibula fused proximally and distally in aged *Tenrec* (unique among lipotyphlans?).

^l Consult Thewissen (1990) for information on incidence of astragalar foramen.

TABLE 3
Character States of *Plesiorycteropus* According to Patterson (1975), Compared to States in Some Other Mammals (II)^a

<i>Plesiorycteropus</i>	*Condy-larthra	Oryctero-podidae	Manidae	Dasypodidae	Tenrecidae
CS1	0	0	①	0	0
CS2	0	0,①	①	1	0
CS3	0	0	①	0	1
CS4	①	①	1	0	1
CS5	①	①	0	1	1
CS6	0,①	0	0	1	1
CS7	①	0	①	1	1
CS8	0,1	①	0	0	1
CS9	①	①	0	1	0
CS10	①	0	0	0,1	1
CS11	0	0	1	0,1	0
CS12	?	①	0	0	0
CS13	0,①	0	①	1	1
CS14	1	0	1	1	1
CS15	0,①	①	1	1	0
CS16	0	0	0	0,1	0
CS17	①	0,①	0	1	1
CS18	①	①	1	1	0
CS19	0,①	①	0	0	0
CS20	0	①	1	1	0
CS21	①	①	①	0	1
CS22	①	①	0	1	1
CS23	0,①	0	0	0	1
CS24	①	①	0	1	1
CS25	0	0	0	0	1
CS26	0	0	①	1	0
CS27	0	0	①	1	0
CS28	0	①	0	0	0
CS29	1	0	1	1	1
CS30	0	0	0	1	1
CS31	0	0,①	1	1	1
CS32	①	①	0	1	1
CS33	0,1	0	0	①	0
CS34	0,1	0	1	1	1
CS35	0	0	1	1	0
CS36	0	0	0	①	0
CS37	0	0	0	1	0
CS38	0,①	0,①	0	1	0
CS39	0	0	1	1	0
CS40	0,1	①	0	0	0
CS41	0,1	0	1	1	1
Explicitly stated matches (all ①s)	17	19	8	2	0
All matches (all 1s + ①s)	24	19	20	30	22

^a Characters abstracted from table 2, polymorphic characters included: 0 = no match; 1 or ① = match with *Plesiorycteropus*; 0,1 or 0,① = polymorphic (counted as match). Totals are column sums. See text for additional details.

is a derived feature of that particular genus. (Presumably, *Plesiorhycteropus* would be counted as being even more derived, but in a different direction.) Thirdly, it is especially unclear whether we are to accept that the tubulidentate hypothesis sensu Patterson succeeds because of the sheer number of resemblances between *Plesiorhycteropus* and Orycteropodidae (and their presumed ancestors in *Condylarthra), or because a few "important" characters demonstrate that this is the only reasonable conclusion. My own sense is that Patterson chiefly relied on numbers. Characters that he should reasonably have viewed as important (i.e., as highly derived with limited distributions among Eutheria), such as position of the mandibular fossa, form of the distal ulna, and characters of the astragalus, are treated very briefly and without due regard to how different from true orycteropodids *Plesiorhycteropus* really is. By contrast, reams of traits of arguably minor significance are invoked (e.g., presence of postglenoid foramen, inclination of occipital, projection of deltopectoral area), seemingly for the purpose of instantiating that "[all] in all, there is a strong similarity between condylarths and aardvarks [including *Plesiorhycteropus*] in the skeleton . . ." (Patterson, 1975: 232).

For all these reasons, Patterson's stated analyses and comparisons are not compelling by themselves. A more complete framework for considering distributions is required in which *all* potential cross-matches are identified and counted (second line of totals in table 3). While I acknowledge that there is room for argument about some of my trait assessments, I find that the most striking result of filling empty cells is that the expanded concordance *ceases to point explicitly in the direction of orycteropodids and condylarthrans*:

(1) Counting all "as in P" character states (and polymorphies), as matches, *Plesiorhycteropus* can be said to agree with *Condylarthra in 24 instances and with Orycteropodidae in 19—as before, both significant counts. The surprising fact, however, is that now the orycteropodid count is *exceeded* by each of the other three groups with modern representatives: manids display 20 resemblances, tenrecids 22, and Dasypodidae a remarkable

30. Thus Patterson's own character set—expanded only in the sense that all necessary comparisons are actually made—falls far short of supporting his principal argument, that *Plesiorhycteropus* is unambiguously related to aardvarks.

(2) Turning the comparison around, we now find that there are only 4 character states (PCS 12, 19, 28, and 40) shared by *Plesiorhycteropus* and *Condylarthra and/or Orycteropodidae that are *not* found in one or more of Manidae, Dasypodidae, or Tenrecidae. By contrast, manids display no fewer than 7 character states (PCS 1, 3, 11, 26, 27, 35, 39) that occur in *Plesiorhycteropus* but not in either *Condylarthra or Orycteropodidae—although it is also true that all but one of these occur in other taxa in the table. Another comparison of interest is that nearly half (9/19) of the matches between *Plesiorhycteropus* and *Orycteropus* also occur in Tenrecidae, the taxon introduced to provide an outgroup perspective.

Why, then, did Patterson prefer the tubulidentate hypothesis over its competitors? No doubt the absence of any cingulate fossils—or even anything that Patterson would have accepted as "edentate" in 1976—in the Old World was a sufficient basis, in his mind, for rejecting any evolutionary connection between *Plesiorhycteropus* and dasypodids or other xenarthrans. It is somewhat more difficult to understand why he rejected out of hand the possibility that *Plesiorhycteropus* was closer to Pholidota than Tubulidentata. This would appear to have been a viable alternative, especially biogeographically: if one believes that an aardvark could raft from Africa to Madagascar, why not a pangolin? Patterson himself noted that there are several respects in which *Plesiorhycteropus* is much more like pholidotans than any known tubulidentate. For example, the cranial features of *Plesiorhycteropus* that Patterson (1978) listed as representing major departures from aardvark morphology—short face, lack of postorbital process, mandibular fossa isolated on a ventrally directed process of the squamosal, and probable reduction or absence of teeth—are found in this combination in manids alone among mammals. However, he maintained that such traits were not significant because they were mere habitus adap-

tations, repeated again and again in mammalian myrmecophages having no close evolutionary relationship with one another.⁴

THEWISSEN: THE TUBULIDENTATE HYPOTHESIS REVISITED

As far as I am aware, J. G. M. Thewissen (1985) is the only author who has made an original investigation of *Plesiorcyteropus* since the appearance of Patterson's (1975, 1978) papers. Thewissen's (1985) study is limited to features of the skull, cephalic vasculature, and brain, and takes the form of a preliminary challenge to the hitherto widely accepted argument that Tubulidentata and Ungulata (or some subset thereof) are sister taxa. Although part of his paper is taken up by a presentation of new evidence concerning the morphology of *Plesiorcyteropus*, this evidence is used primarily to anchor character analyses within Tubulidentata. *Plesiorcyteropus* itself is accepted as a tubulidentate without discussion. Evaluations of characters are generally presented in a format appropriate for cladistic analysis, but no cladograms or tabular presentations of derived traits of tubulidentates are provided. Character state distributions are selectively provided for Ungulata, Tubulidentata, Xenarthra, and Lipotyphla (and a variety of groups not con-

sidered here), and many of the character states are assessed for their primitiveness or derivedness. Superclade Ungulata includes condylarthrans, tacitly regarded as paraphyletic, and usefully broken down by genus in assessments of character distributions.

In rather marked contrast to Patterson's essentially unqualified support for a primitive ungulate derivation of tubulidentates, Thewissen (1985) concluded that the evidence does not strongly favor this or any other conclusion regarding aardvark affinities. He did not himself offer or discuss any alternative phylogenetic arrangements for tubulidentates, pointing out that critical evidence is lacking for many relevant groups.

Although Thewissen (1985) was not attempting to deal with the question of the monophyly of *Plesiorcyteropus* + Tubulidentata, I find that his analysis offers little in the way of solid support for a sister-group relationship between these two taxa. Table 4 presents, for *Plesiorcyteropus* and *Orycteropus* only, 20 of the characters discussed by Thewissen (1985). Not represented is most of the information which he provides on brain/endocast features, little of which was analyzed for cladistic purposes. Entries in roman (plain) type identify characters for which *Plesiorcyteropus* and *Orycteropus* are either primitive or differ between themselves; bold-face distinguishes those characters that are shared and derived according to Thewissen. In some instances he indicates more than one possible interpretation of polarity, and I have simply chosen the one that I believe is consistent with the facts as he presents them. However, I disagree with some of Thewissen's character state assessments (see Morphology of the Cranium), and my interpretation is placed after his, in bracketed italics.

Using Thewissen's character states (TCS), I find that there are five synapomorphies that could be used to support a sister-group arrangement of *Plesiorcyteropus* and *Orycteropus*—TCS 3, 10, 13, 15, and 20. A sixth, TCS 2, could be counted if *Plesiorcyteropus* is more derived than (but on the same morphocline as) *Orycteropus* in degree of stapedial reduction, and a seventh (TCS 17) if loss of the caudal tympanic process of the petrosal is morphotypic for *Plesiorcyteropus* (species of which are variable in this regard). This

⁴ The comparative morphological basis for myrmecophagy in *Orycteropus* is remarkably slim, as Patterson (1975: 220) realized: "[A] combination of osteological characters . . . permits ready recognition of any extinct myrmecophage possessing it, but it must be observed that on these criteria one could not be sure that *Orycteropus* was a committed myrmecophage were it only known from the fossil state. This genus has fully functional molars and posterior premolars and a high ascending ramus . . . [it] stands in striking contrast to *Plesiorcyteropus* with its rather pangolin-like jaw articulation." Patterson had no ready explanation for this contrast, which he aptly described as a "very curious anomaly," except to retreat into the teleological argument that *Orycteropus* had to keep teeth and other impedimenta of nonmyrmecophages for some overarching adaptive reason. The one that he suggested—a peculiar dietary requirement that can only be met by consumption of a kind of cucumber—is remarkable chiefly for its implausibility. *Plesiorcyteropus*, on the other hand, was apparently under no such prior constraint and was free to specialize fully on ants and termites, becoming rather manidlike in the process.

TABLE 4
Selected Cranial Characters of *Plesiorycteropus* and *Orycteropus* (After Thewissen, 1985)

Characters and character states ^a	<i>Plesio- rycteropus</i>	<i>Orycteropus</i>
1. Rhinencephalon size (0, large; 1, small)	0	0
*2. Stapedial artery completeness (0, unreduced; 1, reduced to supraorbital branch [of maxillary]; 2, absent)	2 [0]	1
3. Internal carotid position (0, medially positioned; 1, laterally positioned)	1	1
4. Exit of internal carotid from tympanic cavity (a, through membrane; b, through basisphenoid)	? ^b	b
5. Frontal emissary foramen (a, absent/drains diploic spaces only; b, drains dorsal sagittal sinus)	b	a
6. Commissural vein presence (0, present; 1, absent)	1	0
7. Temporal sinus (postglenoid foramen) presence (0, present; 1, absent)	0	1
8. Rostral cerebral vein size (a, small; b, large)	b	a
9. Ethmoid foramen size (a, smaller; b, larger)	b	a
*10. Lacrimal size (0, facial portion small; 1, facial portion large) ^c	1 [0]	1 [0]
*11. Lacrimal foramen position (0, intraorbital; 1, extraorbital)	0 [1]	1 [0]
*12. Rotundo-orbital foramen contents (0, contains V2; 1, does not contain V2, which passes through separate foramen rotundum instead)	0 [1]	0
13. Alisphenoid canal presence (0, present; 1, absent)	1	1
14. Large epitympanic sinus presence (0, absent; 1, present) ^d	0	1
15. Subarcuate fossa size (0, large; 1, small/absent)	1	1
*16. Cochlear aqueduct opening (0, dorsally opening; 1, ventrally opening)	0 [1]	1
*17. Caudal tympanic process of petrosal (0, present; 1, absent)	0, 1 [0] ^e	1
*18. Rostral tympanic process of petrosal (0, absent; 1, present)	0, 1	0
*19. Tensor tympani origin (0, mainly alisphenoid; 1, mainly petrosal)	0 [1]	0
20. Foramen ovale position (0, between alisphenoid and petrosal; 1, in alisphenoid)	1	1

^a Numbers (0, primitive; 1, derived) are used if polarity is clearly stipulated by Thewissen (1985); letters (a, b) are used if it is not. Bold numbers identify derived traits (or successively derived states) present in both *Plesiorycteropus* and *Orycteropus*. Asterisks denote disputed traits; my alternative codings are bracketed (see text for details).

^b Character state not specified for *Plesiorycteropus* by Thewissen, although “a” may be implied.
^c I consider Thewissen’s polarities to be reversed. Thus facial portion of lacrimal is large and *primitive* in both taxa.
^d Epitympanic sinus not scored as present in *Plesiorycteropus* because Thewissen’s identification of a pneumatic foramen cannot be supported.

^e According to Thewissen, MNHNP 327 lacks both petrosal tympanic processes, which are present in MNHNP 328, so characters 17 and 18 are scored as polymorphic. (See, however, Material, Taxonomy, and Occurrence.)

would appear to provide some support for Patterson’s tubulidentate hypothesis, but there are some problems. For example, I conclude from my own investigations that, contra Thewissen (1985), there is ample evidence that *Plesiorycteropus* possessed a ramus superior (TCS 2; see Morphology of the Cranium, Vascular Features). Evidence for the ramus inferior and ramus posterior is equivocal. Accordingly, with respect to TCS 2, the appropriate character state for *Plesiorycteropus* is either 0 or 1, but not 2. I also differ from Thewissen (1985) in my assessment of the morphology relating to TCS 16 (cochlear

aqueduct opens ventrally in *Plesiorycteropus* also). In this case, reassessment leads to an additional potential synapomorphy since both taxa now express the putatively derived state. (Morphological reassessments of TCS 11, 12 and 19 in table 4 change the character state for *Plesiorycteropus* or *Orycteropus*, but do not yield new synapomorphies.) It may also be noted that the primitive position of the internal carotid (TCS 3) in Eutheria is controversial (see Wible, 1987; MacPhee et al., 1988; Rougier et al., 1992), as is the primitive condition of foramen ovale (TCS 20; see Rose and Emry, 1993) and the size of the facial

wing of the lacrimal (TCS 10; see Novacek, 1986). Which of these characters should be deleted from the final count of synapomorphies is, of course, dependent on which are regarded as being acceptably polarized, but in any case there is not much that inspires confidence. Unpolarized vascular features such as TCS 5 and 8 merit further study, but inasmuch as the two target taxa never display the same character state, there would be no synapomorphous basis for defining a sister-group relationship even if polarity were known. Once again, we must conclude that if *Plesiorhycteropus* is a tubulidentate, this fact is not overridingly obvious from its skull.

SUMMARY

It is plain from this short history that *Plesiorhycteropus* is not very much like any other eutherian, extant or extinct. Lamberton's (1946) attribution of *Plesiorhycteropus* to *Edentata may strike modern readers as objectionable, but Patterson's (1975) confident assertions about tubulidentate relationships seem no more convincing. *Plesiorhycteropus* clearly fails to resemble closely any of the groups to which it has so far been compared. It is unsettling that competent systematists have favored, as close relatives of *Plesiorhycteropus*, taxa that are nowadays usually relegated to opposite ends of the eutherian cladogram. In my view, there is a necessary standard of analysis that has not been met in previous attempts to define the systematic place of *Plesiorhycteropus*; it is the object of this study to provide it.

METHODS AND MATERIALS

The information collected in this monograph is designed to shed light on the relationships, morphology, and adaptations of *Plesiorhycteropus*. The next major section (Material, Taxonomy, and Occurrence) reviews the existing hypodigm of *Plesiorhycteropus* and provides diagnoses of the genus and its constituent species (including a new species), using all information currently available. These housekeeping sections are followed by chapters on cranial and postcranial morphology and matters related to function, adaptation, and extinction of *Plesiorhycteropus*. The final chapter considers, via phylo-

genetic analyses, various choices for the seating of *Plesiorhycteropus* within Eutheria. Because of the incompleteness of the hypodigm in certain important respects, and because of great uncertainty concerning the identity of the sister taxon of *Plesiorhycteropus*, I have tried to make the most of what is available and to follow whatever leads the evidence offered. As a consequence, there is much more morphological information in the descriptive sections than proved utilizable in the character analysis.

Although Lamberton's (1946) description of the skeleton of *Plesiorhycteropus* was careful and detailed, he overlooked many features of significance and considered function only incidentally. Patterson (1975), by contrast, largely confined himself to brief comparisons, and Thewissen's (1985) treatment was limited to certain cranial and endocast features. None of these papers is well illustrated, and a major goal of this presentation is to provide the first adequate photographic atlas of the skeletal anatomy of *Plesiorhycteropus*.

The chief purpose of the descriptive sections is to provide information for the character analyses presented in the last section. Many skeletal features of *Plesiorhycteropus* have no or uncertain counterparts in other eutherians, and for this reason they need to be explored in detail. Descriptions pertinent to discussion of features listed in Characters and Transformations (see The Systematic Position of *Plesiorhycteropus*) are flagged in boldface. For example, C 1, a character concerning the size of the optic canal, is referenced in Morphology of the Cranium, Foramina of Orbit.

Another convention that will be followed in the text is to precede, with an asterisk, the names *Condylarthra and *Edentata. This will signify that the groups in question are not regarded as monophyletic. However, in order to provide some latitude in usage where phylogenetic concepts may not be directly at issue, I do not apply this convention to the English derivatives of these names (e.g., edentate, condylarthran). The ambit of *Condylarthra is described in a subsequent paragraph. *Edentata is understood to include Xenarthra + Pholidota + Tubulidentata, among orders with extant representatives. *Edentata in Novacek's (1986) more restrict-

ed sense (Xenarthra + Pholidota), weakly founded on morphological evidence, is not employed in this paper.

Any mammal that displays detailed morphological resemblances to Xenarthra, Pholidota, Tubulidentata, and primitive ungulates is not likely to present an easy subject for cladistic analysis. Choice of relevant outgroups using the criteria of Maddison et al. (1984) is particularly difficult given the span of alleged relatives just outlined, and mandates a very wide range of comparisons indeed. In the text, the term "comparative set" refers to the taxon assemblage used for most morphological comparisons (table 5). The central taxa in the comparative set include ones that have been historically viewed as having the greatest number of perceived phenotypic resemblances to *Plesiorhycteropus*. These are extant aardvarks, armadillos, and pangolins, together with some of their fossil relatives, and several groups within *Condylarthra, the admittedly paraphyletic umbrella sheltering phenacodonts, meniscotheres, peripitychids, hyopsodonts, and (depending on author) certain other early Tertiary primitive ungulates. Understanding their relationships with one another and with other mammals would obviously benefit from phylogenetic analysis, a task being undertaken by others (e.g., Thewissen and Domning, 1992). The prospects of *Condylarthra surviving as a formal nomen for a monophyletic group are dim (cf. Thewissen and Domning, 1992). However, in the descriptive sections it would be useful for economy of reference to have a general term for primitive ungulates (including the four groups named above), and paraphyletic *Condylarthra is acceptable for that purpose. Most of my comparisons are based on the literature and some original study of meniscotheres, phenacodonts, and hyopsodonts, the taxa best represented cranially and postcranially in AMNH collections.

Vermilinguans and sloths have always been tangential to the debate concerning the relationships of *Plesiorhycteropus*, but they have to be referenced because any conclusions about the systematic significance of the latter's resemblances to armadillos have to be reviewed within the context of supposed sister-group relationships within Xenarthra. However, I have not been as assiduous in

illustrating their morphology as I have been for dasypodids. I also have not checked morphological statements concerning *Bradypus* and *Choloepus* against conditions in any extinct sloths. Once again, my rationale is that "test" comparisons did not lead to any appreciable insights. Thus references in the text to "sloths" must be understood in a restricted sense (i.e., living diversity only).

To these groups I add two others not previously considered by other authors—Hyracoidea and Lipotyphla. There is currently much debate about the near relationships of hyraxes (e.g., Prothero et al., 1988; Fischer, 1986; McKenna, 1992), but there is general agreement that they are part of the great ungulate "bush" (cf. Novacek et al., 1988). Hyraxes are included in this study for the same reason that lipotyphlans are, which is that members of these groups display some unusual and possibly derived similarities to *Plesiorhycteropus*, heretofore unappreciated.

Ultimately there are practical limits to the number of comparisons that can be made, and accordingly some taxonomic entities will not be treated here despite arguments that might be made for their putative relevance. One of these is Palaeanodonta. Palaeanodonts and *Plesiorhycteropus* both display some truly remarkable similarities to xenarthrans, but they also evince some substantial departures (e.g., no accessory intervertebral joints) which are so basic to the diagnosis of Xenarthra that their absence cannot be ignored (for recent discussions of palaeanodont morphology and relationships, see Rose et al., 1991, 1992; Rose and Emry, 1993). In any event, just because palaeanodonts and *Plesiorhycteropus* resemble xenarthrans in some ways does not imply that they especially resemble each other. Traditional ungulate groups other than the ones noted above are not considered (including pantodonts, arctocyonids, mesonychids, cetaceans, and sirenians), although certain taxa are referenced in relation to specific morphological or functional traits.

Following Shoshani et al. (1988) and other recent authorities, I recognize only one extant species of aardvark, *Orycteropus afer*. Colbert (1941: 310) claimed that the nominal subspecies *O. a. aethiopicus* "shows certain resemblances to the extinct, Pliocene types—in other words, it is seemingly more primi-

TABLE 5
Chief Taxa Utilized for Morphological
Comparisons (Comparative Set)^a

Lipotyphla
Soricomorpha
<i>Tenrec ecaudatus</i> (tenrec; Madagascar)
<i>Solenodon paradoxus</i> (almiquí; Hispaniola)
<i>Solenodon cubanus</i> (almiquí; Cuba)
Erinaceomorpha
<i>Echinosorex gymnura</i> (moonrat; SE Asia)
<i>Hylomys suillus</i> (lesser gymnure; SE Asia)
Rodentia
Muridae
<i>Hypogeomys antimena</i> (votsovoetsa; Madagascar)
Tubulidentata
Orycteropodidae
<i>Orycteropus afer</i> (aardvark; Africa)
† <i>Orycteropus gaudryi</i> (Miocene, Eurasia)
Hyracoidea
Procaviidae
<i>Procavia capensis</i> (rock dassie; parts of Africa, Near East)
<i>Heterohyrax brucei</i> (gray hyrax; central Africa)
<i>Dendrohyrax dorsalis</i> (tree hyrax; central Africa)
Pholidota
Manidae
<i>Manis crassicaudata</i> (Indian pangolin; S. Asia)
<i>Manis javanica</i> (Javan pangolin; S. Asia)
<i>Manis tricuspis</i> (tree pangolin; Africa)
<i>Manis tetradactyla</i> (ground pangolin; Africa)
<i>Manis gigantea</i> (giant pangolin; Africa)
† <i>Patriomanis americanus</i> (E. Oligocene, N. America)
Xenarthra (extant taxa restricted to S. America, except <i>D. novemcinctus</i>)
Vermilingua
Myrmecophagidae
<i>Myrmecophaga tridactyla</i> (three-toed anteater)
<i>Tamandua tetradactyla</i> (four-toed anteater)
<i>Cyclopes didactylus</i> (silky anteater)
Tardigrada
Bradypodidae
<i>Bradypus tridactylus</i> (three-toed sloth)
<i>Bradypus variegatus</i> (three-toed sloth)
Megalonychidae
<i>Choloepus hoffmanni</i> (ai-ai)
Cingulata
Dasypodidae
<i>Euphractus sexcinctus</i> (six-banded armadillo)
<i>Priodontes maximus</i> (giant armadillo)

TABLE 5—(Continued)

<i>Cabassous unicinctus</i> (southern naked-tailed armadillo)
<i>Tolypeutes tricinctus</i> (northern three-banded armadillo)
<i>Dasypus novemcinctus</i> (nine-banded armadillo)
Stegotheriidae
† <i>Stegotherium tessellatum</i> (E. Miocene, S. America)
*Condylarthra (referenced taxa N. American)
Meniscotheriidae
† <i>Meniscotherium terraerubrae</i>
Phenacodontidae
† <i>Phenacodus</i> spp.
Hyopsodontidae
† <i>Hyopsodus paulus</i>
Peripitychidae
† <i>Ectoconus majusculus</i>

^a For extant species, taxon names and content follow Wilson and Reeder (1993). Although proposals to subdivide *Manis* continue to be made, I follow Heath (1992) in including all extant pangolin species under this generic name. Not all of the taxa listed above are utilized in the parsimony analyses described in the last section. Likewise, many more taxa than the ones listed were used in adjudicating polarities, as discussed under individual entries in the character analyses.

tive. . . .” Study of relevant material in the AMNHM collections convinces me that what differences there are (e.g., frontal sinus size) must be allometrically conditioned as Colbert (1941) himself noted. In any case, most of the contrasts among nominal subspecies of *O. afer* seem trivial and will not be considered in detail in this paper. For information on extinct aardvarks I have mostly relied on Patterson (1975) and other pertinent literature. For *Orycteropus gaudryi* I have utilized papers by Andrews (1896), Lönnberg (1906), and Colbert (1941), supplemented by original comparisons with specimens in the AMNHP collections.

In subsequent sections, Orycteropodidae is to be understood as the taxon that includes *Orycteropus*, *Myorycteropus*, and *Leptorycteropus*, and is thus equal in content to Patterson’s (1975) Orycteropodinae. I have no reason to doubt that this nominal taxon is

monophyletic, because all accepted members are known for *certain* to share one exclusive synapomorphy of tubulidentates—teeth composed of tubulodentine. This is not known for other alleged Tertiary tubulidentates; none of these merit consideration here, with the sole exception of *Leptomanis* which is of interest for a quite different reason (see Appendix I). Used alone, the terms “Tubulidentata,” “tubulidentates,” and “aardvarks” will refer to orycteropodids (in my sense); for the sake of clarity, I shall use the convention “Tubulidentata + *Plesiorycteropus*” when it is necessary to make joint reference to tubulidentates and the Malagasy subfossil.

Although it was not feasible to illustrate every element of every member of the comparative set and other pertinent taxa, I have tried to include a good sampling of line illustrations so that readers without ready access to a good mammalogical collection can easily follow comparisons made in the text. The following specimens were used as models for these drawings: *Amblyrhiza inundata* AMNHP 11843, astragalus; *Bradypus variegatus* AMNHM 42838, femur; *Dasybus*

novemcinctus AMNHM 211666, skull, pelvis, femur, astragalus; *Dendrohyrax dorsalis* AMNHM 53814, astragalus; *Echinosorex gymnura* AMNHM 32640, humerus, pelvis, femur; *Euphractus sexcinctus* AMNHM 70092, humerus, radius, ulna, pelvis; *Heterohyrax brucei* AMNHM 82103, skull; *Macaca nemestrina* AMNHM 11091, pelvis; *Manis crassicaudata* AMNHM 244407, humerus, radius, ulna, pelvis, tibiofibula, astragalus; *M. tetradactyla* AMNHM 53866, skull; *Meniscotherium* sp. AMNHP 4414, astragalus; *Orycteropus afer* AMNHM 51235, skull, humerus, pelvis, tibiofibula, femur, astragalus; *O. afer* 51905, radius; *Procavia capensis* AMNHM 53781, humerus, radius, ulna, pelvis, femur, tibiofibula; *Solenodon cubanus* AMNHM 35330, skull; *S. paradoxus* AMNHM 212912, radius, ulna; *Tamandua tetradactyla* AMNHM 211658, skull, humerus, ulna, radius, femur, tibiofibula, astragalus; *Tenrec ecaudatus* AMNHM 30398, humerus, tibiofibula; *T. ecaudatus* AMNHM 212913, pelvis, femur, astragalus; and *Ursus americanus* AMNHM 144885, astragalus.

MATERIAL, TAXONOMY, AND OCCURRENCE

HYPODIGM

Lamberton (1946) and Patterson (1975) briefly summarized information then available on the hypodigm of *Plesiorycteropus*, and gave their reasons for concluding that only one kind of mammal is represented in the remains that they considered to represent *Plesiorycteropus*. Neither of them provided a complete list of specimens, which is here provided in table 1. As this table demonstrates, the most substantial collections of *Plesiorycteropus* are housed in the Institut de Paléontologie (MNHN) and the Laboratoire d'Anatomie Comparée (MNHNA) of the Muséum National d'Histoire Naturelle in Paris. Unfortunately, the documentation accompanying most specimens of *Plesiorycteropus* is minimal, and for a significant number there is no provenance at all.

From an accounting standpoint, the skeletal parts of *Plesiorycteropus* are about as well

represented in collections as those of several of the lesser-known subfossil lemurs (e.g., *Daubentonia robusta* [Lamberton, 1934; MacPhee and Raholimavo, 1988]). As has already been noted, there are skulls, but none retains its facial skeleton. Each of the major long bones is represented by at least one essentially complete specimen (several in the case of femora and humeri), but there is no definitive evidence that any two of them came from the same individual. The pelvis is also represented by several specimens, but the single scapula (MNHNA 1987.034) that might belong to *Plesiorycteropus* is really too fragmentary for definite allocation. Except for the cervical region, the spinal column is moderately well known, although not well enough to establish the complete vertebral formula with any certainty. The most significant remaining gaps in our knowledge of the postcranium concern the manus and pes: wrist

and ankle elements are unknown (with the exception of the astragalus), as are most of the metapodials and phalanges. Likewise, no clavicles, ribs, or sternal elements have been identified. However, such gaps as there are will probably be closed in short order, thanks to efforts by David Burney, Helen James, and co-workers. They recently collected, at Anjohibe in northwestern Madagascar, the first new specimens of *Plesiorycteropus* documented since the 1930s (Burney et al., in press).

The closest approximation to an associated "skeleton" of *Plesiorycteropus* is the series of elements recovered by the collector Geay at Ambolisatra. Lamberton (1946: 32 [trans.]) specifically noted that Geay recovered, "near the skull fragment with nasals preserved. . . , four lumbar, five caudals, and a sacrum still in connection with the pelvis. It seems highly likely that all these elements belong together, and it is not impossible that they all pertain to a single individual." The Ambolisatra pelvic girdle can no longer be located, but the other elements were found in the Madagascar collections of the MNHNP. The Ambolisatra skull and free vertebrae each bear the original accession number "1905-8." In the MNHNP catalog, this numerical sequence is set next to a notation, "mission du Muséum, 21 janvier." Next to this is a taxon list and an indication of the number of elements cataloged per taxon; one entry in this list is "oryctérope (?), 3." The "oryctérope" entry is puzzling, since there are more attributable elements than this enumeration implies. One of Geay's three "oryctérope" specimens was doubtless the partial cranium with attached nasals (now MNHNP 534); the others may have been an ulna, also numbered "1905-8" (now MNHNP 330), and perhaps the sacrum with associated innominates, now lost. A much less likely possibility is that Geay actually found additional skulls (or parts of skulls), but these were lost or misplaced before they could be described.

A single individual is doubtless represented by the skull and postcranial bones recovered in 1992 by Burney et al. (in press) at their site 8 within the cave system at Anjohibe (table 1). There are no duplicates in this material, which was found at or near the surface within a dried-out rimstone pool (H. James, personal commun.)

Finally, a number of elements attributable to *Plesiorycteropus* now in the MNHNA collections were not referenced in Lamberton's (1946) or Patterson's (1975) accounts. The largest group of such elements was associated with a card bearing the following information: "ossements d'*Hypogeomys* trouvée par M^r et M^{me} [blank space follows] Village de l'Amboza Ankazoabo—Don de M^r B. Le [illegible] 1929." These elements were located in a drawer with lemur bones donated by G. Grandidier, and have evidently been overlooked by other workers.

TAXONOMY

Lamberton (1946) noted the existence of substantial morphological and metrical variation in his sample of *Plesiorycteropus*, but he did not attempt to resolve whether this implied that more than one species existed during the Recent of Madagascar. My review of the evidence indicates that recognition of a second species is warranted. In the next section, this new species is defined and the diagnosis of *P. madagascariensis* emended accordingly.

In view of the systematic conclusions reached in the last section of this monograph, "Madagascar aardvark" is not an appropriate common name for *Plesiorycteropus*. As a replacement I recommend the manufactured common name "bibymalagasy," which I shall use henceforth (for derivation, see below).

PLESIORYCTEROPUS Filhol, 1895

Content: *Plesiorycteropus madagascariensis* Filhol (1895), type species, and *P. germainepetterae*, new species.

SYNONYMS: *Majoria* Thomas (1915: 57, footnote) (= *Myoryctes* Forsyth Major [1908], preoccupied), new synonymy; *Hypogeomys* [parte] G. Grandidier (1912).

ETYMOLOGY: Greek comb. form *plesio*- ("near") + *Orycteropus* (extant genus of aardvarks).

RECOMMENDED COMMON NAME: Bibymalagasy (sing. and plur.), from Malagasy *biby* ("animal") + *malagasy* ("Malagasy," "of Madagascar"), and pronounced approximately BEEB-mala-GASH.

EMENDED DIAGNOSIS: Filhol's (1895) diagnosis of *Plesiorycteropus* is inadequate and neither Lamberton (1946) nor Patterson

(1975) provided a genus-level definition *per se*, an omission that I now repair. This diagnosis should be read in conjunction with the final section of this paper, The Systematic Position of *Plesiorycteropus*.

Plesiorycteropus is a eutherian distinguished from all other known eutherians (including all recognized tubulidentates) by the following combination of nonprimitive features: (1) mandibular fossa large and flat, restricted to facies articularis of squamosal (i.e., with no involvement of the zygomatic process of squamosal); (2) nasals markedly widened rostrally; (3) neural arches of posterior thoracic and all lumbar pierced by large longitudinal channels (transarcual canals), here interpreted as venous channels; (4) ischial tuberosities highly modified, expanded, and caudally flattened (may have borne specialized dermal structures); and (5) posteromedial process of astragalus present and very large (may have acted as a pulley for flexor tibialis).

MORPHOLOGICAL SUMMARY: For ready reference, I provide here a morphological catalog of the major features of *Plesiorycteropus*, additional to those made part of the diagnosis: (6) skull with comparatively long neurocranium and short face; (7) ethmoid labyrinth apparently large, with complex turbinal system and associated paranasal sinuses; (8) ossified nasal septum extending almost to margin of external nasal aperture; (9) lacrimal facial wing large, lacrimal foramen located immediately inside orbital rim; (10) cranio-orbital foramen present; (11) transpromontorial internal carotid artery present; (12) complete proximal stapedial continuing into braincase as the ramus superior, ramus inferior and (more doubtfully) ramus posterior possibly present; (13) percranial canal for great diploetic artery apparently present; (14) sulcus present for occipital artery in relation to percranial canal; (15) small tympanic process of pterygoid (rest of tympanic floor occupied by ectotympanic, either alone or in combination with one or more entotympanics); (16) separate foramen rotundum (V2) and sphenoorbital foramen (V1), the former much the larger; (17) ethmoid foramen very large, probably drained superior sagittal sinus as well as ethmoid region; (18) subarcuate fossa negligible; (19) true mastoid foramen absent; (20) postorbital process absent; (21) post-

glenoid process absent, mandible back-stopped by small preotic crest functioning as a pseudoglenoid process; (22) jaws possibly edentulous (masticatory apparatus unknown); (23) laminae of lumbar neural arches display progressive and marked decrease in rostrocaudal depth; (24) medial epicondyle of humerus not greatly expanded, deltopectoral eminence large; (25) ulna with very long lever arm (triceps process), shaft narrowing distally to tiny ulnocarpal joint surface; (26) radius shaft broad and flattened, with wide distal articular end, lunate facet much larger than scaphoid facet; (27) pelvic girdle transversely narrow, with sharply downturned, gracile pubes and very small pubic symphysis; (28) ischial tuberosity expanded into a large, flat plate; (29) femoral greater trochanter extends well cranial from head; (30) femoral lesser trochanter very prominent, subquadrilateral with unusually large and well-defined area for quadratus femoris insertion; (31) femoral third trochanter large, situated near middle of lateral surface; (32) patellar surface wide and nearly flat; (33) tibia and fibula fused both proximally and distally; large cnemial crest extending down to middle of tibial shaft; (34) distal tibial articular surface transversely wide but anteroposteriorly narrow; (35) medial malleolus large and projecting, with separate condylar facet for articulation with cotylar fossa on medial aspect of astragalus; (36) astragalus with very shallow trochlea, short undeviated neck, distinct but very small ental facet and no astragalal foramen; (37) known metapodials short but robust, with large heads; (38) known proximal and intermediate phalanges very short and broad; (39) unguals transversely narrow and pointed, not hooflike.

Plesiorycteropus madagascariensis
Filhol, 1895

HOLOTYPE: MNHN 328 (fig. 2), a partial cranium with several cranial sutures still open (probably subadult or young adult).

DISCOVERER AND DATE OF DISCOVERY: M. Grevé, in or before November, 1894 (cf. A. Grandidier, 1895).

TYPE LOCALITY AND AGE: Unlocated Quaternary site in "grey alluvial sands" (Milne-Edwards and A. Grandidier, 1895) near Belo, central west coast of Madagascar.

SYNONYMS: *Majoria* (= *Myoryctes*) *rapeto* Thomas (1915), **new synonymy**; "*Hypogeomys*" *boulei* G. Grandidier (1912).

REFERRED SPECIMENS: Partial associated skeleton from Ambolisatra, southwestern coast of Madagascar (MNHN 534, calvarium; MNHN 540–543, lumbar vertebrae; MNHN 1714–1718, caudal vertebrae; unlocated pelvic girdle); NHMLP M 7085, nearly complete innominate from Antsirabe, central Madagascar (holotype of *Majoria rapeto*); MNHN 1987.038, nearly complete femur from Ampasambazimba, central Madagascar (holotype of "*Hypogeomys*" *boulei*); and USNM 474080, skull lacking facial region, many sutures open.

ETYMOLOGY: *madagascariensis*, "of Madagascar."

DIAGNOSIS: Differs from smaller *P. germainepetterae* n. sp. (q.v.) in the following combination of traits: (1) braincase larger and less globose; (2) orbital constriction less pronounced; (3) temporal lines higher; (4) pseudoglenoid process less prominent; (5) small ?vascular foramen absent adjacent to foramen ovale; (6) rostral and caudal tympanic processes of petrosal more developed; (7) temporal tubercle faint; (8) dorsal profile of nuchal crest straight; and (9) third trochanter of femur larger.

DISCUSSION: Measurements of holotypes of *Majoria rapeto* and *Hypogeomys boulei* (table 12) place them in the upper end of ranges observed for *Plesiorycteropus*, indicating that these specimens represent *P. madagascariensis*.

***Plesiorycteropus germainepetterae*,
new species**

HOLOTYPE: MNHN 327 (fig. 5), a partial cranium lacking facial region, with most sutures obliterated (and therefore definitely adult).

DISCOVERER AND DATE OF DISCOVERY: Unknown.

TYPE LOCALITY AND AGE: "Centre d'île, Madagascar" according to Lamberton (1946). In Lamberton's works this phrase usually denotes Ampasambazimba, a well-known locality that he excavated during the mid-1920s, although he sometimes used the same phrase

to refer to sites in the environs of Antsirabe (Chanudet, 1975; MacPhee et al., 1985).

SYNONYMS: None.

REFERRED SPECIMENS: MNHN 329, a complete femur, provenance unknown.

ETYMOLOGY: For Dr. Germaine Petter of the MNHN.

DIAGNOSIS: Differs from *P. madagascariensis* in being smaller overall (by 8–19% for linear measurements) and in the following combination of traits: (1) braincase smaller and more globose; (2) orbital constriction more pronounced (extends across cranium); (3) temporal lines lower; (4) pseudoglenoid process more prominent; (5) small ?vascular foramen present adjacent to foramen ovale; (6) rostral and caudal tympanic processes of petrosal less developed; (7) temporal tubercle prominent; (8) dorsal profile of nuchal crest indented; and (9) third trochanter of femur smaller.

DISCUSSION: Lamberton (1946) noted the existence of size differences in skulls of *Plesiorycteropus* but refrained from naming a second species of bibymalagasy. While it may be argued that many of the differences seen could simply be due to individual or sex-related variation, the contrast in braincase size alone between MNHN 327 and 328 is a compelling justification for recognition of *germainepetterae* and *madagascariensis* as separate species (see Morphology of the Cranium and table 8).

At this stage it is not possible to differentiate the geographical ranges of *Plesiorycteropus madagascariensis* and *germainepetterae*. The holotype of *P. madagascariensis* comes from Belo on the west coast (fig. 1), but the referred cranial fragment (MNHN 534) is from the far south, the referred femur (MNHN 1987.038) is from Ampasambazimba in the central highlands, and the new skull from Anjohibe (USNM 474080) is from the northwest. The only provenanced specimen referred to *germainepetterae* is the holotype from "centre d'île," but many of the smaller postcranials from various sites in southern Madagascar may also prove to belong to this species (although except for MNHN 329 they are not specifically so allocated here). On this evidence, the apparent ranges of these species overlapped extensive-

ly. Significant range overlap among closely related species is seen elsewhere in the Malagasy subfossil record (e.g., *Aldabrachelys* [= *Testudo*] *grandidieri* and *A. robusta*; *Megaladapis grandidieri* and *M. edwardsi*). No apparent "ecogeographic gradient" in skull size exists in the available bibymalagasy sample, although such gradients apparently occur in skulls of certain extinct lemurs according to Godfrey et al. (1990) and Albrecht and Miller (1993).

MISALLOCATED SPECIMENS

Individual skeletal elements of *Plesioryc-teropus* display remarkable similarities to their counterparts in a wide assortment of mammalian taxa that stand far apart phylogenetically, biogeographically, or both. In the past, these similarities led some workers to suggest allocations that are now seen to be erroneous. These misallocations will be of interest to workers dealing with other Malagasy mammals, and are presented in summary form below.

SPECIMENS MISALLOCATED TO RODENTIA

The inaptly named "extinct Madagascan mouse" (Anderson, 1984), *Majoria rapeto*, is based on a nearly complete innominate found by Forsyth Major at a site near Antsirabe, probably in 1895. Forsyth Major (1908) thought that this specimen was similar to pelvises of Malagasy nesomyines, but he made no subfamilial allocation. He (1908: 97) noted several features of the specimen that could be correlated with digging adaptations, and concluded that he would "not hesitate in assigning the fossil to a highly fossorial rodent." Except among muroid specialists (e.g., Carleton and Musser, 1984), Forsyth Major's (1908) paper has attracted no attention and was overlooked by both Lamberton (1946) and Patterson (1975). The facts are that the holotype of *Majoria rapeto* is identical in every way to innominates assigned to *Plesioryc-teropus*, and that despite damage to the ischium it is the best-preserved representative of this element now known.

The holotype of "*Hypogeomys*" *boulei* (G. Grandidier, 1912), now accessioned as

MNHNA 1987.038 (fig. 34), is a large femur from Ampasambazimba that is fully preserved except in the area of the lateral condyle. Despite its size, G. Grandidier (1912) argued that this specimen was so similar to the femur of the extant nesomyine *H. antimena* (Malagasy, *votsovoetsa*) that it warranted placement in the same genus. Lamberton (1946) expressed some hesitation in allocating this and other femoral specimens of a similar type to the hypodigm of *Plesioryc-teropus*. However, he pointed out that if a "giant" *votsovoetsa* had existed during the Malagasy Quaternary, it was very odd that no other distinctively nesomyine-like bones in its size range had been recovered. In the end he referred all of these large, unusual femora to *Plesioryc-teropus*, a decision that Patterson (1975) endorsed and I have no hesitation in accepting.

It should be noted that the other "giant" *votsovoetsa* described by G. Grandidier (1903), *H. australis*, is only 10–20% larger in linear measurements than extant *H. antimena*, and is therefore far too small to be relevant here. (Size was confirmed on two specimens in the MNHNP collections, MNHNP 1646 [partial mandible] and 1647 [partial maxilla].) That *H. australis* is only slightly larger than the living species is not obvious from Lamberton's (1946: pl. 3, figs. f, g) side-by-side illustrations of *Hypogeomys* femora. His figure f probably does represent a femur of *H. australis* if, as stated by Lamberton, the photograph is reproduced at natural size. But his figure g, said to be of *H. antimena*, is only half the size of the undoubted *antimena* femora in the collections of the MNHNZ (e.g., MNHNZ CG 1984-651). It must therefore belong to some other, smaller nesomyine.

SPECIMENS MISALLOCATED TO PRIMATES

The hypodigm of *Daubentonina robusta* as assembled by Lamberton (1934) unquestionably belongs to a large aye-aye (cf. MacPhee and Raholimavo, 1988), and his allocations are not in question here. The problematic specimen is instead a partial innominate (PMU M 5095) from Masinandrana that Ekblom (1953) referred to this extinct lemur.

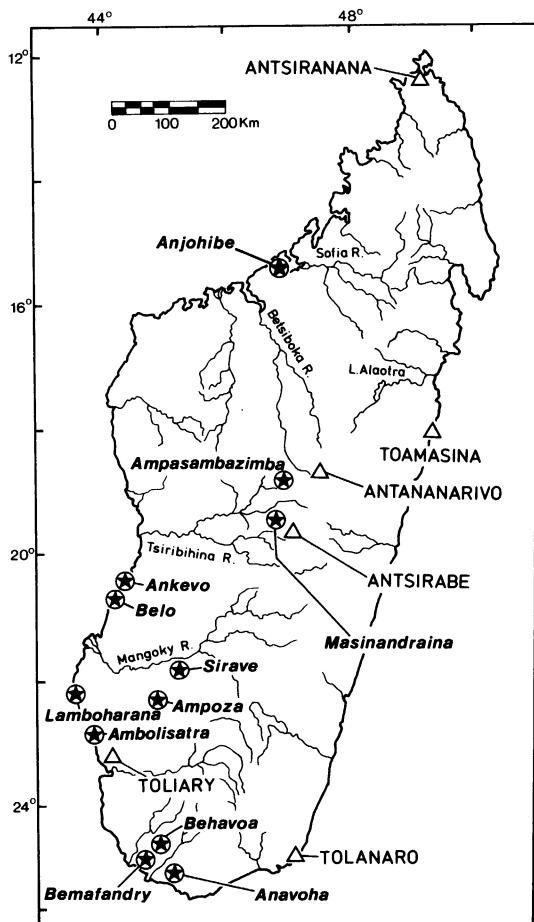


Fig. 1. Subfossil localities yielding provenanced specimens of *Plesiorycteropus*. Spellings of sites (stars) and major towns (triangles) have been altered in some cases to conform to modern usage (see Introduction, List of Abbreviations).

This specimen differs from the *D. robusta* innominate described by Lamberton (1934) in several ways, most of which were in fact detailed by Ekblom (1953) in his description. The most obvious difference, easily made out by comparing photographs in their respective papers, is the immense size of the projecting iliopectineal eminence in the Masinandraina specimen, which exactly replicates the equivalent feature in innominates referred to *Plesiorycteropus*.

MacPhee and Raholimavo (1988) noticed Ekblom's (1953) misallocation but, having

wrongly concluded that some elements in the hypodigm of *Plesiorycteropus* indicated a connection with tenrecs, described this specimen as belonging to a "giant tenrecoid."

For completeness, it may be noted here that the incomplete femur from Ambolisatra mentioned by Forsyth Major (1894: 31) as bearing "a striking resemblance with a *Manis* femur" probably belongs to the extinct lemur *Palaeopropithecus*, not *Plesiorycteropus*.

REJECTED SPECIMENS

The last section of table 1 lists specimens that were associated with the MNHNA and MNHNP material of *Plesiorycteropus* when it came into my hands for study, but which I have concluded do not belong in the hypodigm. The "Village Ampoza" collection also included a few other small bones and fragments that are not referenced in the table. These are either not *Plesiorycteropus* or too poorly preserved for identification.

LOCALITIES

Validly referred specimens of species of *Plesiorycteropus* are presently known from a dozen different subfossil sites in central, western, and southern Madagascar (fig. 1). The majority of the provenanced specimens come from Ampoza and Sirave in the south, and from Ampasambazimba and sites around Antsirabe in the central highlands. An adequate analytical guide to the subfossil localities of Madagascar and their contained faunas has never been published, although useful information on some sites can be found in papers by Tattersall (1973), Chanudet (1975), and MacPhee et al. (1985).

Like *Hippopotamus*, *Palaeopropithecus*, *Megaladapis*, and many other extinct taxa that once lived in central and southwestern Madagascar, species of *Plesiorycteropus* seem not to have been uniquely tied to forest biotopes now restricted to the western and eastern sides of the island. How could they have existed amid the depauperate grasslands that cover the interior of the island? The explanation may be that the Quaternary fauna was largely confined to narrow belts in and around the major wetlands—swamps, river margins,

and lakes—that still abound in the interior (although usually without much associated forest). This is supported by the fact that the *only* subfossil localities found in the interior

are in wetland settings (MacPhee, 1986). The disappearance of *Plesiorhycteropus* is taken up in a later section (see Function, Adaptation, and Extinction).

MORPHOLOGY OF THE CRANIUM

With the discovery of the new partial cranium from Anjohibe (Burney et al., in press), the number of *Plesiorhycteropus* skulls available for study becomes four (MNHN 327, 328, and 534, and USNMP 474080; figs. 2–5). The Anjohibe specimen is especially welcome because it appears to be the youngest of the four judging from the extent of suture closure, and thus helps to clear up some doubts about composition (e.g., presence of interparietal). Regrettably, all specimens are more or less extensively damaged. Patterson (1975) stated that one skull—evidently the one now cataloged as MNHN 327 (fig. 5)—had not been seen by Lamberton (1946), but I agree with Thewissen (1985) that this specimen is identical to the one Lamberton described as being in the “Musée de Tananarive” (i.e., Akademia Malagasy). That is, it was once identical, but has since suffered considerable damage, having lost most of the cribriform plate, lacrimals, and occipital, as well as small pieces from the orbital and basicranial regions. MNHN 328 (fig. 2), the holotype of *P. madagascariensis*, has also suffered: in his diagnosis Filhol (1895) made reference to the “strong zygomatic arch” of this specimen, but by the time Lamberton studied this skull nothing remained of this structure on either side. Additional cleaning of these skulls has revealed some new details, particularly in the area around the cranio-mandibular joint. In the following descriptions, skulls will be identified by museum accession number or by locality (see table 1).

A point of some taphonomic interest is that all four skulls lack the rostral parts of the face; indeed, three of the four skulls are broken in almost precisely the same place, i.e., through the large paranasal spaces that frame the anterior end of the neurocranium. Presumably, the walls bounding these spaces were comparatively thin and easily fractured, suggest-

ing that the face as a whole was rather lightly built. By contrast, the bones of the neurocranium and posterior orbit are thick and unpneumatized, and tend to fuse along sutural boundaries, explaining why this part of the bibymalagasy skull tends to survive intact. The factor responsible for breakage (e.g., sediment pressure, predator manipulation) is not ascertainable.

As previously noted, no teeth or mandibles have been assigned to *Plesiorhycteropus* by previous workers, and I failed to turn up any likely candidates in existing collections.

SKULL SHAPE AND PROPORTIONS

Patterson's (1975) dorsal reconstruction of the bibymalagasy skull (fig. 10A) depicts a rather globose neurocranium, lacking prominent muscle scars, that narrows anteriorly at the orbital constriction, widens again across the posterior nasal cavity, and then terminates in a comparatively short facial region. Each of these features can be documented from the available cranial material. Patterson went further, however, and also sketched in his idea of the outlines of the zygomatic arch and facial region as they might appear in an intact skull. The zygomatic arch is depicted as being formed by two processes that fail to meet, a strongly built zygomatic process of the maxillary and a more gracile zygomatic process of the squamosal. The reconstructed outline of the dorsal portion of the face suggests a rapidly narrowing, blunt rostrum.

Patterson's (1975) dorsal reconstruction is plausible, but it involves some suppositions that require scrutiny. He clearly felt that the skull of *Plesiorhycteropus*, in its shape and proportions, was more like that of *Orycteropus* than that of any other mammal. We may begin to evaluate this by examining some measurements. Measurements, actual or es-

TABLE 6
Plesiorycteropus: Cranial Measurements (in mm)

MNHNP 327 (<i>Plesiorycteropus germainepetterae</i>)	
1. Fronto-occipital length ^a	66.0 ^c
2. Frontal length ^b	29.5
3. Interorbital width ^c	25.1
4. Braincase width ^d	36.2
MNHNP 328 (<i>Plesiorycteropus madagascariensis</i>)	
1. Fronto-occipital length	71.4
2. Frontal length	34.8
3. Interorbital width	26.3
4. Braincase width	38.0
USNMP 474080 (<i>Plesiorycteropus madagascariensis</i>)	
1. Fronto-occipital length	76.1
2. Frontal length	38.3
3. Interorbital width	24.7
4. Braincase width	36.6
MNHNP 534 (<i>Plesiorycteropus madagascariensis</i>)	
1. Fronto-occipital length	—
2. Frontal length	33.2
3. Interorbital width	27.7
4. Braincase width	—
5. Nasals, maximum width between alae	10.3
6. Nasals, minimum width at nasofrontal suture	5.3
7. Nasals, length (posteriormost point on nasofrontal suture to plane intersecting alae)	27.1
8. Maximum length of specimen	77.4

^a Posteriormost point on nasofrontal suture toinion (maximally posterior point on nuchal crest).

^b Nasofrontal to coronal suture (nasion to bregma, in midsagittal plane).

^c Minimum width (dorsal aspect).

^d Maximum width above plane of squamosal zygomatic processes.

^e Estimate, with allowance for small loss of bone from nuchal crest and from nasofrontal suture.

timated, of available bibymalagasy skulls are provided in tables 6 and 7, together with comparative data for some other taxa. Greatest "dorsal" skull length in *Plesiorycteropus madagascariensis* may be tentatively set at approximately 10 cm (nasal length + fronto-occipital length, combining measurements for the Belo, Anjohibe, and Ambolisatra skulls). Fronto-occipital length is approximately 9% less in the single representative of *P. germainepetterae*, MNHNP 327, in which the frontal is disproportionately short compared with that of the *madagascariensis* specimens. Obviously, *Plesiorycteropus* was a much

smaller animal than *Orycteropus afer* or even extinct *O. gaudryi* (table 7). The index of fronto-occipital length to braincase width (VI/V in table 7), as a measure of braincase shape, indicates that the bibymalagasy braincase is about twice as long as it is wide. This is a similarity not only to *Orycteropus* but also to most other members of the comparative set (with the exception of *Manis*, which has a notably higher index). Lack of strong muscular scars on the dorsal aspect of the cranium is also a widely distributed feature in mammalian groups lacking enlarged temporal musculature.

While it might be argued that differences between *Plesiorycteropus* and *Orycteropus afer* are due to allometry, this proposition seems unlikely in view of the fact that *O. gaudryi*—also smaller than *O. afer*—is nevertheless quite similar in proportions to the living aardvark. Thus in the species of *Orycteropus* the rostrum (as represented by nasal length) constitutes almost half of "dorsal" skull length as measured by the ratio II/I (table 7), but in *P. madagascariensis* it is considerably less than one-third. The parietals are rostrocaudally longer than are the frontals; parietals subequal to or longer than frontals is a primitive feature (C 8).

A smoothly tapering muzzle is as characteristic of dasypodids and manids as it is of orycteropodids—and of myrmecophagids, although in this group the length and strength of the taper are carried to a derived extreme (fig. 6). In all these groups, the taper is contributed by the same factors: on the one hand, by the relative gracility of the whole rostrum (narrow palate, weak alveolar borders); on the other, by the marked pneumatization of the air chambers in the posterior nasal cavity (ethmoid labyrinth, maxillary sinus, frontal sinus). These jointly produce the outward bulging of the whole preorbital part of the facial skeleton and rapid narrowing of the rostrum. It is reasonable to suppose that *Plesiorycteropus* had a similar aspect, as Patterson suggested, but the result cannot be described as exclusively aardvarklike. As Patterson also noted, in general shape the bibymalagasy skull departs substantially from that typical of condylarthrans, although it might be argued that much of the difference is due to the fact that in known condylarthran

TABLE 7
Plesiorhycteropus and Comparative Set: Cranial Measurements (in mm) and Ratios

Taxon ^a	Measurements and Ratios ^b						II/I (%)	IV/III (%)	VI/V (%)
	I	II	III	IV	V	VI			
<i>Plesiorhycteropus madagascariensis</i>	101.0 ^c	27.1	35.4	37.2	73.8	37.3	26.8	105.1	50.5
<i>Plesiorhycteropus germainepetterae</i>	—	—	29.5	35.5	66.0	36.2	—	120.3	54.8
<i>Orycteropus afer</i>	222.1	95.0	61.3	58.6	126.5	63.3	43.7	95.6	50.0
<i>Orycteropus gaudryi</i>	175.0 ^c	77.0 ^c	45.9	45.0 ^c	—	47.5	44.0	98.3 ^c	—
<i>Manis tetradactyla</i>	65.0	24.5	21.3	16.5	39.1	29.1	37.7	77.7	74.4
<i>Dasyus novemcinctus</i>	96.0	30.2	42.6	17.9	64.6	30.7	31.5	42.0	48.2
<i>Tolypeutes matacus</i>	73.4	16.7	32.3	22.8	57.8	24.4	22.8	70.6	42.2
<i>Tamandua tetradactyla</i>	122.5	39.9	48.9	23.6	84.9	43.6	32.6	48.3	51.4
<i>Echinosorex gymnura</i>	76.1	29.1	20.5	16.3	47.3	26.4	38.2	79.5	55.8
<i>Dendrohyrax dorsalis</i>	102.8	27.3	34.6	32.4	76.2	35.8	26.6	93.6	50.0

^a For each taxon, N = 3 except in case of *Orycteropus gaudryi* (N = 1) and *Plesiorhycteropus* (see next footnote).

^b I, greatest "dorsal" skull length (in the midsagittal plane, anteriormost projection of nasal bones to maximally projecting point on the nuchal crest). II, nasal length (in midsagittal plane, anteriormost projection of nasal bones to frontonasal suture [nasion]). For *P. madagascariensis*, MNHNP 534. III, frontal length (in midsagittal plane, nasofrontal suture [nasion] to coronal suture [bregma]). For *P. madagascariensis*, average of MNHNP 328 and 534 and USNMP 474080. IV, parietal/interparietal/dorsal supraoccipital length (in midsagittal plane, coronal suture [bregma] to lambdoid suture [lambda]). For *P. madagascariensis*, average of MNHNP 328 and USNMP 474080. V, fronto-occipital length (in midsagittal plane, nasofrontal suture to maximally projecting point on the nuchal crest). For *P. madagascariensis*, average of MNHNP 328 and USNMP 474080. VI, braincase width (maximum width of braincase above plane of zygomatic process of squamosal). For *P. madagascariensis*, average of MNHNP 328 and USNMP 474080.

^c Estimated (see text).

lineages the teeth and jaws are never reduced (and consequently facial structure and muscle markings tend to be comparatively massive).

Perhaps the most controversial aspect of Patterson's (1975) reconstruction is the depiction of the zygomatic arch as interrupted (fig. 10A). There is no direct evidence for arch incompleteness; Patterson's inference is based on the assumed profound reduction of the jaws, which, while reasonable, still needs confirmation.

It is of some interest to set Patterson's (1975) view of the overall organization of the bibymalagasy skull against Lamberton's (1946). Lamberton did not attempt a reconstruction, but he did note that cranial correspondences between *Plesiorhycteropus* and orycteropodids were not especially striking. Against a list of noteworthy similarities to aardvarks (form of occipital region, complete zygomatic arch, coalescence of foramen rotundum and spheno-orbital foramen, absence of tympanic bulla), he set a list of equally substantial departures (smaller rostral part

of face, absence of postorbital process, differing form of frontonasal contact). Even this small list of bibymalagasy-aardvark resemblances goes beyond the available evidence. As noted elsewhere in this section, the foramen rotundum and spheno-orbital foramen are in fact separate (confirmed in *P. germainepetterae*, assumed for *P. madagascariensis*), the completeness of the zygomatic arch cannot be determined from the available material, and the absence of a tympanic bulla is inferential because the tympanic floor is not intact in any specimen.

In sum, therefore, the general shape and proportions of the bibymalagasy skull cannot be described as being overpoweringly similar to those of *Orycteropus*. More detailed assessments of individual cranial regions follow.

FACIAL REGION

Except for the nasals, preserved on MNHNP 534 (fig. 3), and a portion of each

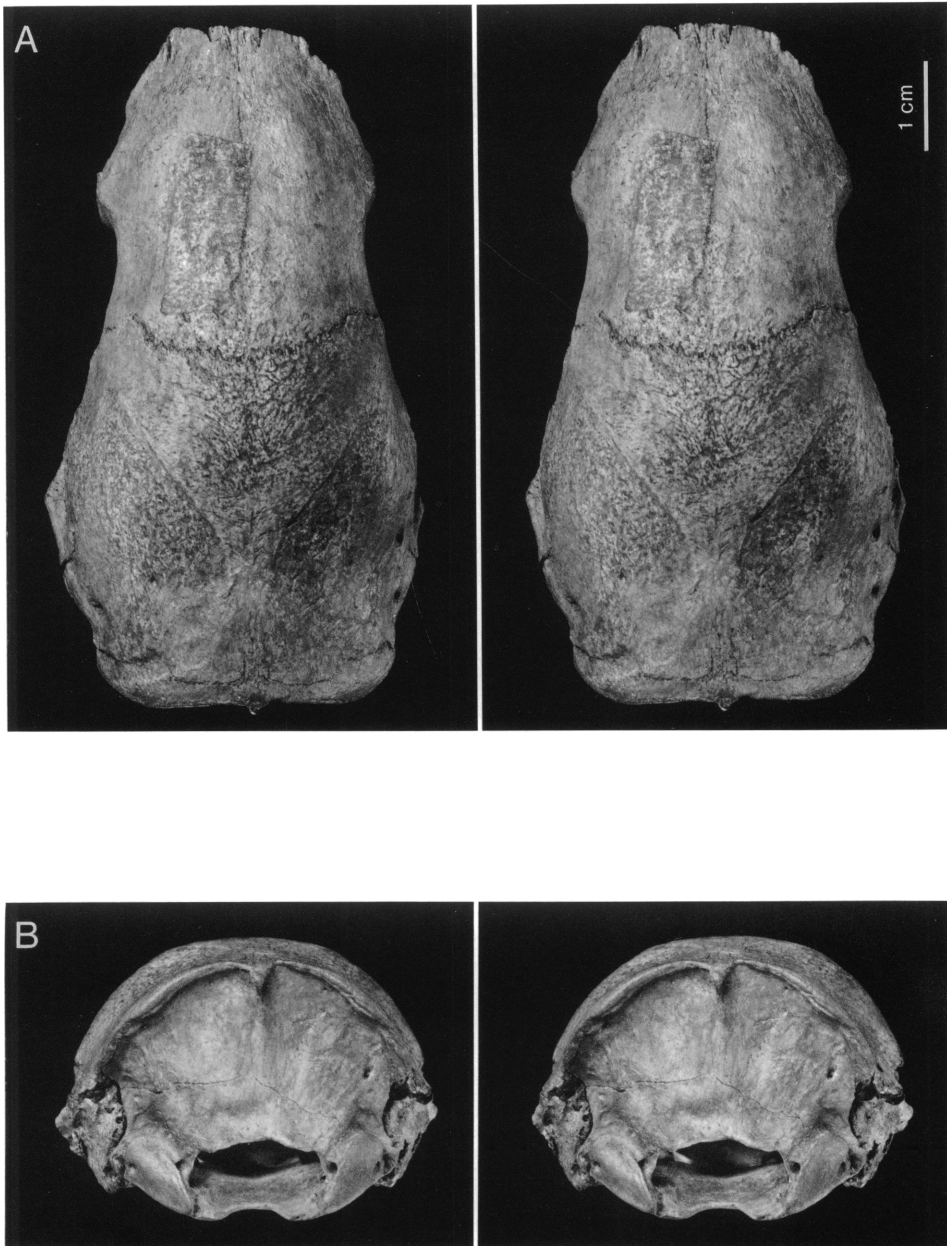


Fig. 2. *Plesiorycteropus madagascariensis* MNHNP 328, holotype (Belo skull). Stereopair views (with keys) on this and following pages: A, dorsal; B, occipital; C, ventral (with enlargement of posterior basicranium); and D, left lateral. All to scale in A. Many cranial sutures were still open at the time of death, but misalignment and improbable width of some sutures is due to later damage. Single asterisk (in ventral key) marks piriform fenestra, enlarged by breakage. Double asterisk (in occipital key) marks approximate position of percranial foramen, enlarged by breakage (aperture intact only in Anjohibe skull; cf. fig. 4B, right side). Fenestra rotunda and sphenorbital foramen appear to be continuous, but in life were separated by a partition, stubs of which remain. Label (visible in A) carries information that fossil was discovered during Grevé's 1895 expedition to Belo.

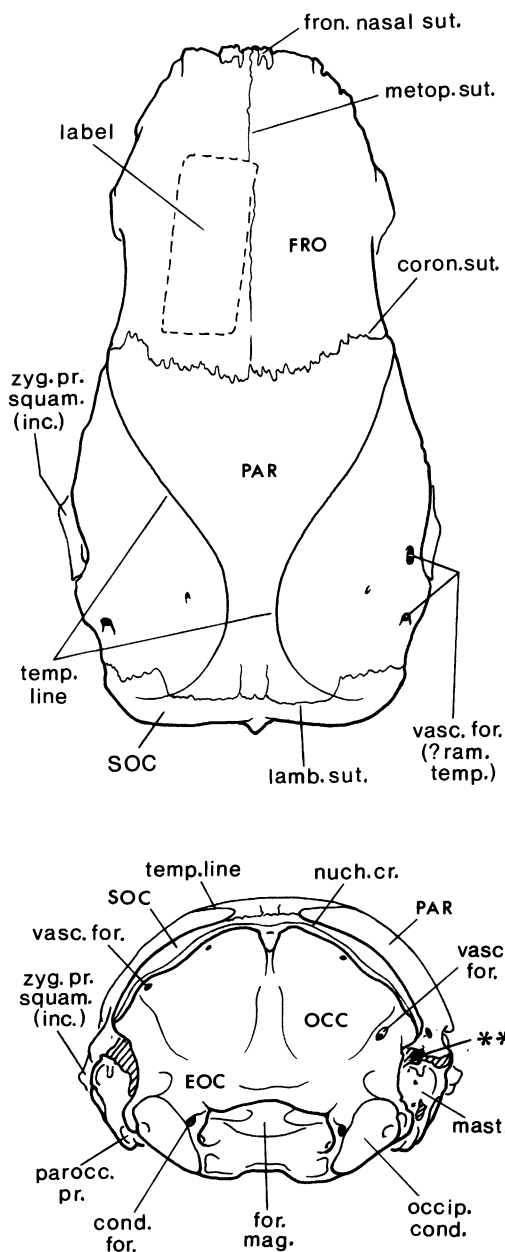


Fig. 2 (continued)

lacrimal, preserved on MNHNP 327 (fig. 5), no part of the bibymalagasy face is known at present.

As both Lamberton (1946) and Patterson (1975) noted, the nasals of *Plesiorhycteropus* are somewhat unusual in their shape and proportions. In MNHNP 534, the two robustly

built nasals form a wedge, deeply set into the frontal, that is approximately twice as wide anteriorly as posteriorly (fig. 3A; table 6). In this specimen the nasofrontal suture is U-shaped, sinuous, and weakly serrated. The concave margin of the nasal aperture is notched in the midline, and the anterior tip of each nasal bone is prolonged anterolaterally into a small ala. Small sections of the frontal part of the frontonasal suture are preserved in the other skulls. Not enough remains in any single case to determine if suture form is variable.

Marked anterior widening of the nasals is uncommon in eutherians. In dasypodids the nasals are anteriorly widened to some extent, although the shape of the border of the nasal aperture is convex rather than concave (fig. 6; C 6). Deep inseting of nasals in the frontal notch is seen in some lipotyphlans (*Erinaceus*) and also in some primitive ungulates (*Meniscotherium*, *Phenacodus*; Gazin, 1965). In *Orycteropus* and *Manis*, the nasals are expanded posteriorly rather than anteriorly and are not so deeply inset into the frontal; in hyraxes, the bones simply abut, and consequently there is no inseting at all (fig. 6). It may be briefly noted that here, as everywhere else in the skull, there is no important resemblance to *Hypogeomys* (see Material, Taxonomy, and Occurrence); *Plesiorhycteropus* obviously lacked the pattern of complicated interdigitations along the nasofrontal suture that is a hallmark of muroid rodents. Perhaps the general robusticity and anterior widening of the nasals in *Plesiorhycteropus* indicate that the mass of the external nose was comparatively large, or that it functioned in digging and rooting, or both of these.

In lateral profile the nasals (fig. 3B) are definitely flatter than in any extant member of the comparative set, including *Orycteropus*. Since teeth are absent in the rostral end of the upper jaw in manids, myrmecophagids, orycteropodids, and armadillos (fig. 6), in these taxa no projecting alveolar ridge is formed and by consequence the forward end of the muzzle is nearly tubular when viewed on end. Whether or not the rostrum of *Plesiorhycteropus* was similarly shaped obviously cannot be determined from the material at hand. The flat profile of the nasals is not necessarily inconsistent with a tubular anterior

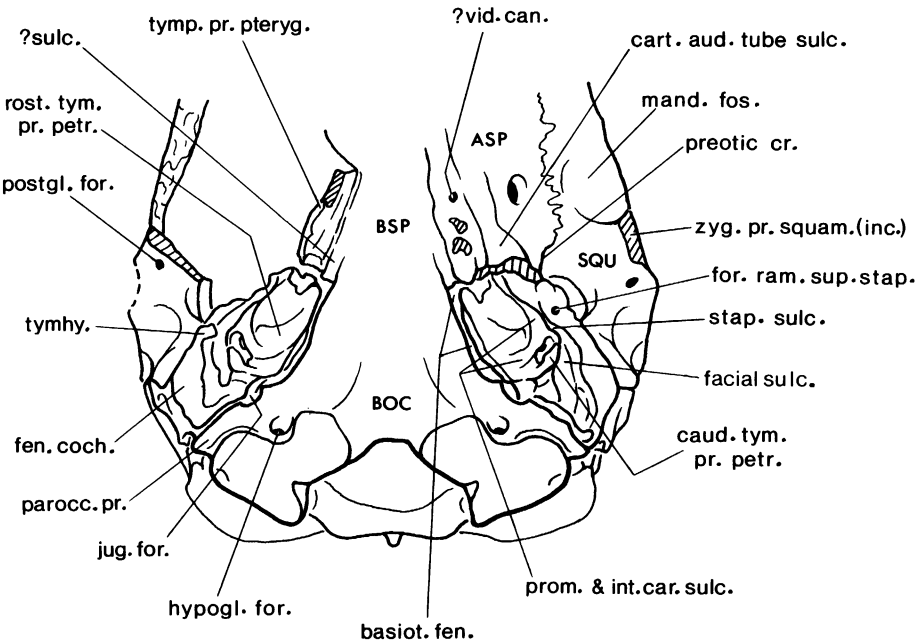
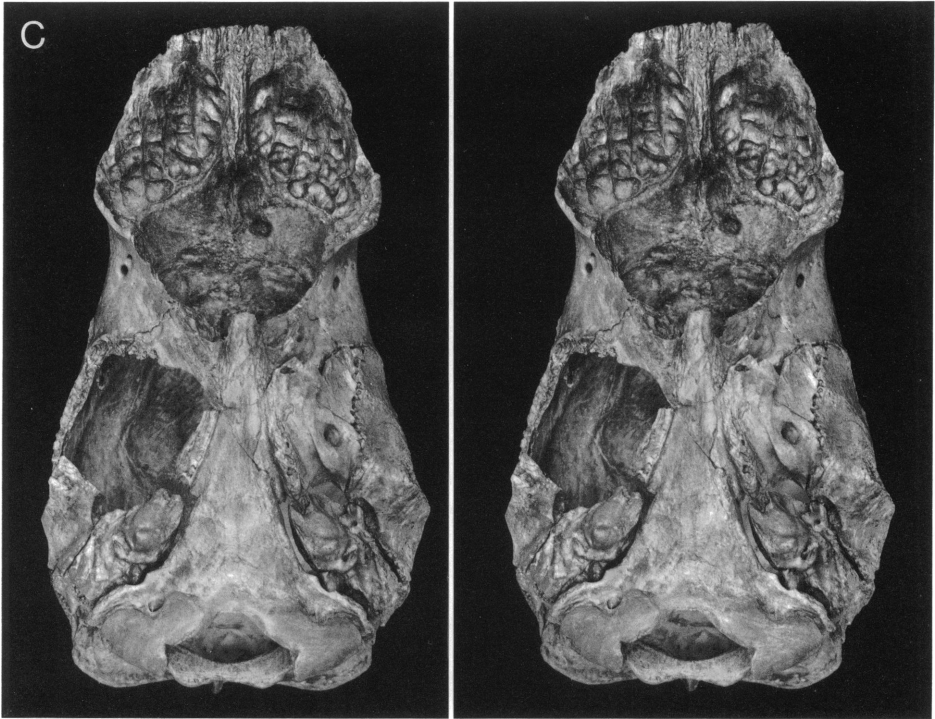


Fig. 2 (continued)

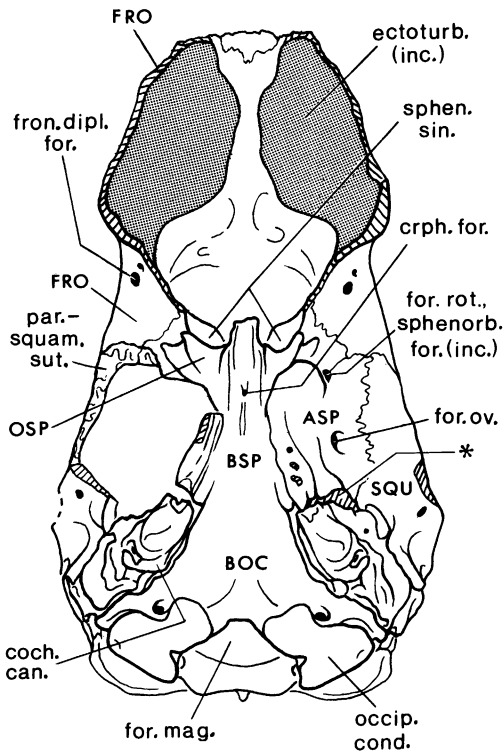


Fig. 2 (continued)

muzzle; *Tolypeutes* has flatter nasals than do other extant armadillos, but its snout is nevertheless suboval in cross-section.

The lacrimals were at least partly preserved on MNHNP 327 at the time that Lamberton (1946) undertook his investigations (fig. 5C, D). These bones were evidently broken off prior to Patterson's (1975: 211–212) study of this specimen, because he was only able to observe the position of the frontolacrimal suture. He inferred that the lacrimal of *Plesiorhycteropus* was probably "comparable in position and relative size to that of *Orycteropus gaudryi*," which implies an element of significant size with large facial and orbital wings (C 4, 5).

At the time of my initial inspection of MNHNP 327, I found several small bone fragments in this specimen's box that obviously belonged to it. Most of these fragments were too small to reattach to the skull, but three of them proved to belong to the lacrimal region on the left side of the skull and one to

the same region on the right side (fig. 5C, D). Although there are large gaps in the reassembly, Patterson (1975) was clearly correct in assuming that the lacrimal of *Plesiorhycteropus* was comparatively large. Sutural contact between the frontal and the lacrimal's orbital wing was squamous above the level of the lacrimal foramen, with the lacrimal extensively overlapping the frontal's anterodorsal edge. The uppermost part of the lacrimal is accordingly broadly visible from the dorsal aspect, as in armadillos and most xenarthrans with elongated rostra (figs. 5A, 6). It seems unlikely that the lacrimal would have contacted the nasals (as they do in *Phenacodus vortmani*, but not *P. intermedius*; Thewissen, 1990). Part of the long intraorbital section of the frontolacrimal suture is open, allowing rough determination of the size of the orbital wing (see below).

As Lamberton (1946) noted, the single, subhorizontal lacrimal canal is situated immediately behind the prominent anterior orbital margin, high on the sidewall of the orbital part of the face (figs. 5C, 11; C 5). Its aperture (lacrimal foramen) lies on or very near the frontolacrimal suture, as in lipotyphlans (Butler, 1956; Thewissen, 1985), in contradistinction to *Orycteropus afer* in which the foramen lies out on the face on the jugolacrimal suture (fig. 6). In *O. gaudryi* the foramen is also positioned low on the facial wing of the lacrimal. In *Plesiorhycteropus* but not *Orycteropus* the entrance to the lacrimal foramen is bordered by a low but quite distinct lacrimal tubercle (cf. figs. 5C, 6). This tubercle is in a position similar to that of *Leptictis* and erinaceomorphs; Novacek (1986) considered it to be absent in nonerinnaceid lipotyphlans (fig. 6). Novacek (1986) also regarded presence of the tubercle as a plesiomorphous trait of edentates, although this feature seems to be of negligible size in most Recent tardigradans and dasypodids (*Euphractus* and *Zaedyus* are exceptions). In myrmecophagids the prominence on the lacrimal is additionally pierced by an arterial canal (evidently for a branch of the "temporal branch of occipital artery" of du Boulay and Verity [1973]; fig. 6), a feature absent in *Plesiorhycteropus*. Lacrimal tubercles have been recorded for *Phenacodus* and *Meniscother-*

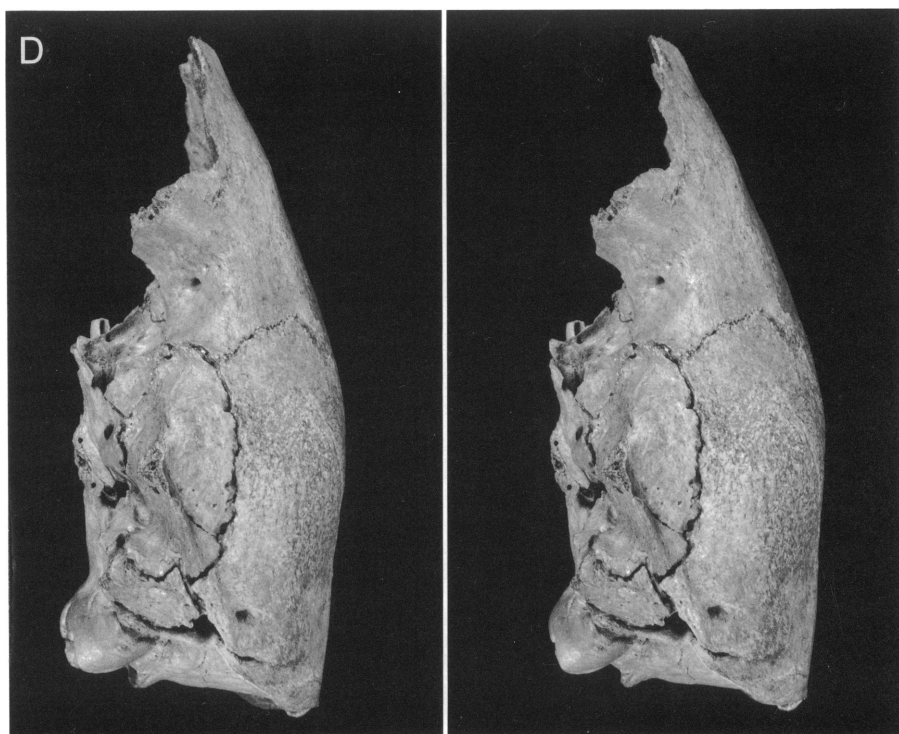


Fig. 2 (continued)

ium (Thewissen, 1990; Thewissen and Domning, 1992). Hyraxes are unusual in having tiny lacrimals surmounted by immense tubercles (fig. 6).

NASAL CAVITY AND PARANASAL SINUSES

NASAL CAVITY

The ethmoid labyrinth seems to have been exceptionally large in *Plesiorhycteropus* (figs. 2–5). This in turn suggests that the potential area for attachment of the sensory olfactory mucosa was also very large (Moore, 1981), and that *Plesiorhycteropus* was accordingly highly macrosomatic. The swollen labyrinth creates two external “bosses” on the exterior aspect of the frontal, separated by a midline dip, a very common feature among mammals. As Colbert (1941) notes, in *O. gaudryi* these swellings are very pronounced, but in living *O. afer* they vary from small to neg-

ligible. In the latter taxon, loss of bossing appears to be correlated with increase in the size of the frontal sinus (?absent in *O. gaudryi*).

Fragments of the dorsal ends of the ectoturbinal lamellae and part of the ossified nasal septum are the only parts of the ethmoid labyrinth that are still preserved on any of the bibymalagasy specimens. Judging from Lamberton's (1946: pl. 1, fig. a') illustration, the cribriform plate of the Ampasambazimba skull (MNHNP 327) was originally almost intact; unfortunately, due to improper handling over the years, only a few fragments of the rim of this structure remain (fig. 5D).

Although the exact number of ectoturbinals cannot be inferred from existing material, the traces of seven or eight separate ectoturbinal lamellae can easily be discerned on the endocranial aspect of the Belo skull (MNHNP 328). Judging from conditions in the better-preserved Ampasambazimba skull, perhaps three or four additional ectoturbinals were

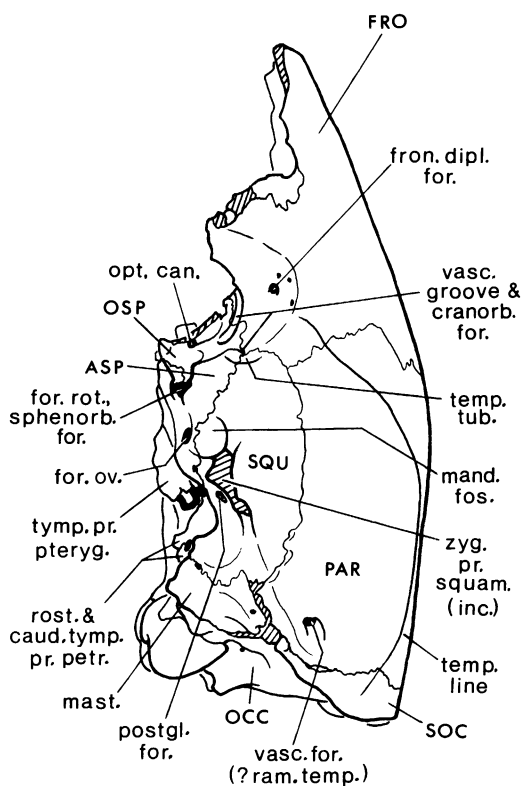


Fig. 2 (continued)

present posteroventrally, within the extension of the labyrinthine airspace into the orbitosphenoid and presphenoid (sphenoid paranasal sinus). In *Orycteropus afer*, as many as 16 or 17 ectoturbinals occupy a roughly equivalent area, judging from Coupin's (1926: 163, fig. 16) portrayal of a dissected adult skull. However, in *Plesiorycteropus* their organization is different, in that the more anterior lamellae are placed almost parasagittally, and individually subtend angles of only 10–20° relative to the midsagittal plane. In *O. afer*, ectoturbinal orientation is much more transverse (50–60° in the specimen illustrated by Coupin (1926: 163, fig. 15). In *O. gaudryi*, lamellar orientation may be somewhat less transverse, although this is difficult to determine from the one available skull in which the ectoturbinals are slightly exposed (AMNHP 20694).

The ossified nasal septum is substantially preserved in the fragmentary *Ambolisatra*

calvarium, MNHNP 534 (fig. 3B, C). The bone that comprises it is remarkably thick and firmly fused to the underside of the nasals, which no doubt explains why it survived while adjacent portions of the skull did not. I assume this to be another mark of advanced ontogenetic age in this skull. The bony septum's ventral surface is flared, presumably for the reception of the absent vomer. Especially remarkable is the fact that the septum extends almost as far as the midline notch on the anterior nasal margin (fig. 3C), i.e., into the zone that in mammals usually remains cartilaginous, as the rostralmost part of the cartilago nasi septi.

In most members of the comparative sample, the cartilaginous septum does not significantly ossify during life, and the bony septum (as the perpendicular plate of the ethmoid) remains restricted to the posterior one-third to one-half of the nasal cavity. In *Manis* the thin bony part of the septum barely extends onto the underside of the nasals, and most of the septum is therefore cartilaginous. In *Orycteropus afer*, the ossified septum is lightly built, extends only about one-third the length of the nasal cavity, and is not fused to the nasal bones. Armadillos are variable; in *Dasybus*, the ossified part of the septum is very short, but in *Tolypeutes* and especially *Priodontes* it is notably longer and better developed. In *Priodontes*, the ossified septum extends more than two-thirds the length of the cavity, although it is not completely fused dorsally to the underside of the nasals. The only taxa I have examined that are substantially similar to *Plesiorycteropus* in degree of septum ossification are *Choloepus* and *Bradypus*. In aged adults, but not in young tree sloths, the septum is ossified almost to the narial opening, and is sometimes completely coossified with the vomer. This similarity, to the degree that it exists, should be assessed in light of the very abbreviated nasal bones of sloths. There is no information on the nature of nasal septum development in extinct primitive ungulates.

The part of the vomer that contacts midline septal structures is usually situated quite low in mammals. This, together with the rather short maximum vertical height of the ossified septum (< 10 mm), implies that the

anterior part of the nasal cavity could not have been very deep.

PARANASAL SINUSES

In the available bibymalagasy skulls, two paranasal sinuses can be identified, a maxillary and a sphenoid. In the Ambolisatra specimen (MNHNP 534), the ectoturbinal lamellae are rostrally bordered by a partition (now broken) that can be traced for a short distance onto the underside of the frontal (fig. 3C). The partition is best interpreted as a part of the dorsal wall of a maxillary paranasal sinus. There is no way to determine from existing evidence how large this sinus may have been, although the presence of tiny lamellae on the intracranial surface of the lacrimals in MNHNP 327 (fig. 5D) implies that this chamber inflated into these bones as well. As noted above, there is no indication of an independent frontal sinus connected to the ethmoid labyrinth.

In the three more complete specimens, fractures also reveal a series of small spaces in the bones of the anterior basicranium (figs. 2C, 4D, 5D), specifically within the presphenoid and orbitosphenoid. Although breakage has destroyed any continuity between these cellules and the ethmoid labyrinth, there can be little doubt that they were in fact once continuous, and that the cellules in the presphenoid and orbitosphenoid represent a sphenoid paranasal cavity (i.e., a caudal extension of the nasopharynx into the bone of the basicranium; Moore, 1981). This interpretation is supported by the position of the cellules and by the stumps of sphenoid turbinates preserved in MNHNP 327 and USNMP 474080.

The rostral extent of the sphenoid paranasal cavity cannot be determined from the material at hand because the bone of the hard palate and posterior nares is not preserved. However, it is clear that inflation must have been extensive, because the body of the presphenoid and the contiguous parts of the orbitosphenoid are markedly puffed out. In this respect the locus and degree of inflation are roughly comparable to conditions in the anterior basicranium of *Dasypus*. In *Orycteropus* the sphenoid sinus excavates the presphenoid (and the palatine) but does not ap-

pear to penetrate the orbitosphenoid. (Le Gros Clark and Sonntag [1926] remarked that the sphenoid sinus is absent in *Orycteropus*, but by this they seem to mean the equivalent of the single, large space usually seen in humans.) *Manis* exhibits little or no sphenoid excavation. *Bradypus* has a profoundly pneumatized skull, but the pattern of pneumatization differs considerably from that exhibited by *Dasypus*. In extant sloths the orbitosphenoid contains a large vacuity, but this is connected to the enormous sinuses that inflate almost the entire dorsum of the neurocranium. In *Dendrohyrax* and other extant hyraxes, the body of the presphenoid is extensively pneumatized, and is connected to pneumatic chambers that puff out the posterior maxillary and orbitosphenoid (but within the orbit rather than on the basicranium per se).

The frontal paranasal sinus as defined by Moore (1981) is completely absent in *Plesiorhycteropus*; it is present and large in *Orycteropus afer*, but may be absent in *O. gaudryi* (see above). I cannot explain Filhol's (1895) comment that *Plesiorhycteropus* has the "same frontal sinus" as an aardvark's, because in *O. afer* this excavation is voluminous (Le Gros Clark and Sonntag, 1926). Hyraxes also have extensive frontal sinuses. Dasypodids vary: *Dasypus* has a large frontal sinus, while *Tolypeutes* seems to lack one altogether. I was not able to ascertain the presence or size of frontal sinuses in myrmecophagids. There is no useful information on paranasal pneumatization in condylarthrans, although Thewissen (1990) has identified frontal pneumatization in *Phenacodus intermedius*.

ORBITAL REGION

ORBITAL MOSAIC

The orbital region is deficient in all of the available bibymalagasy skulls. As seen in lateral view, the orbital cavity is rostrocaudally short compared with the equivalent area in *Orycteropus*, *Tamandua*, *Tenrec*, *Meniscotherium*, and *Phenacodus*, and in this it is similar to the orbital cavities of *Dasypus* and *Manis* (cf. figs. 2–6). The site of maximum neurocranial constriction, as seen in dorsal aspect, is intraorbital, as it is in dasypodids.

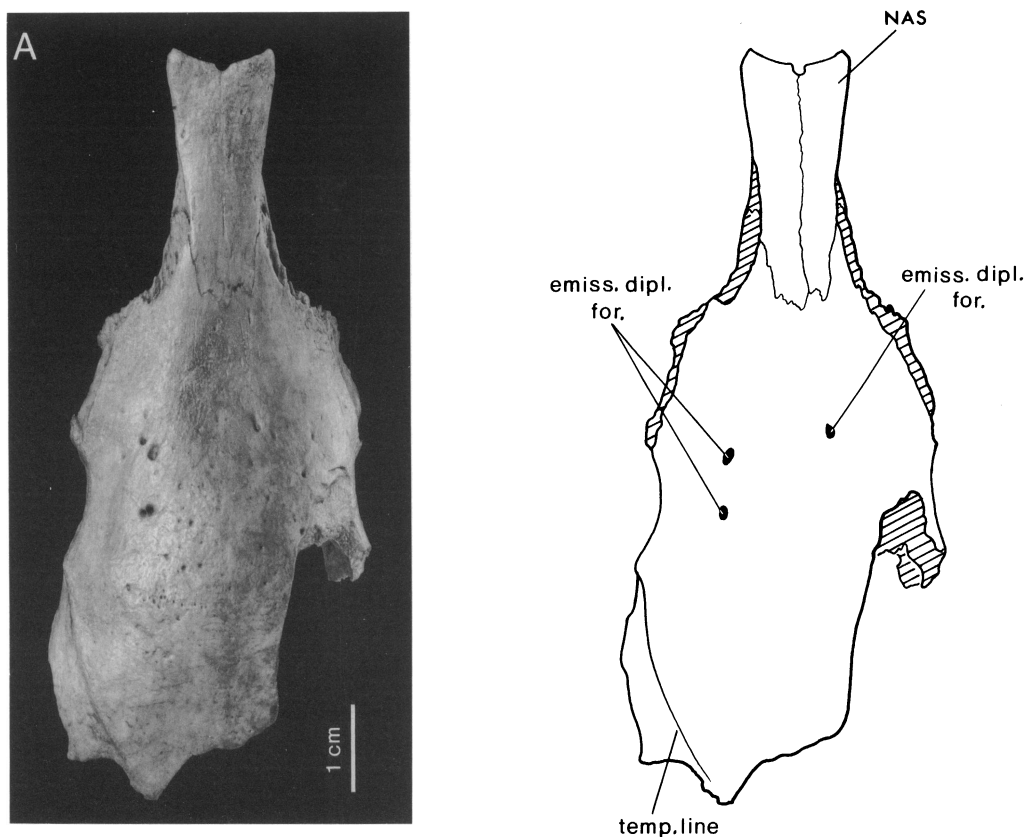


Fig. 3. *Plesiorycteropus madagascariensis* MNHNP 534 (Ambolisatra calvarium preserving nasals). Views (with keys) on this and following pages: A, dorsal; B, left lateral (stereopair) and C, ventral endocranial (stereopair). All to scale in A.

Myrmecophagids are only a little constricted and manids not at all. By contrast, in *Orycteropus* and hyraxes the equivalent site is more posterior, behind the large postorbital tubercles.

Dorsally, the orbital wall in *Plesiorycteropus* is deeply indented, without a sharp margin, and (as preserved in available specimens) appears to be mostly formed by the orbital wing of the frontal. The lacrimal contributes substantially to the orbit's rostradorsal margin. In MNHNP 534, the preserved anterior and ventral borders of the orbital wing of the frontal are finely denticulated and obviously represent intact sutural margins (fig. 3B). The orbital wing of this bone, roughly quadrilateral in form, terminates posteroventrally in a small tablike extension. In bibymalagasy

the frontal did not dominate the orbit to the extent that it does in pholidotans, and in this respect is closer in form to aardvarks, dasypodids (cf. Novacek and Wyss, 1986a), and hyraxes (cf. fig. 6). Anteriorly, the orbitosphenoid is in contact with the posterior part of the orbital wing of the frontal up to the location of the large ethmoid foramen. The orbitosphenoid is conspicuously smaller than in *Orycteropus*, as Patterson (1975) noted. The alisphenoid wing, also relatively smaller than in *Orycteropus*, displays nearly the same degree of development as it does in *Dasypus* (described as "weak" in the case of extant armadillos by Novacek and Wyss [1986a]; C 3).

In MNHNP 327, the inferior border of the orbital wing of the lacrimal is preserved on

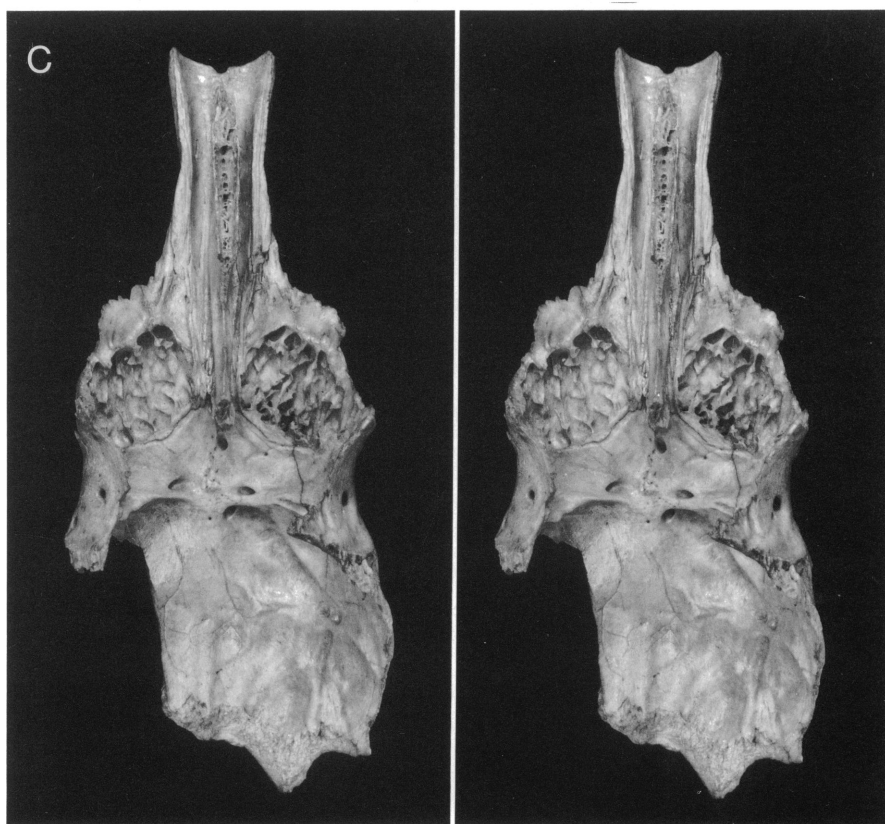
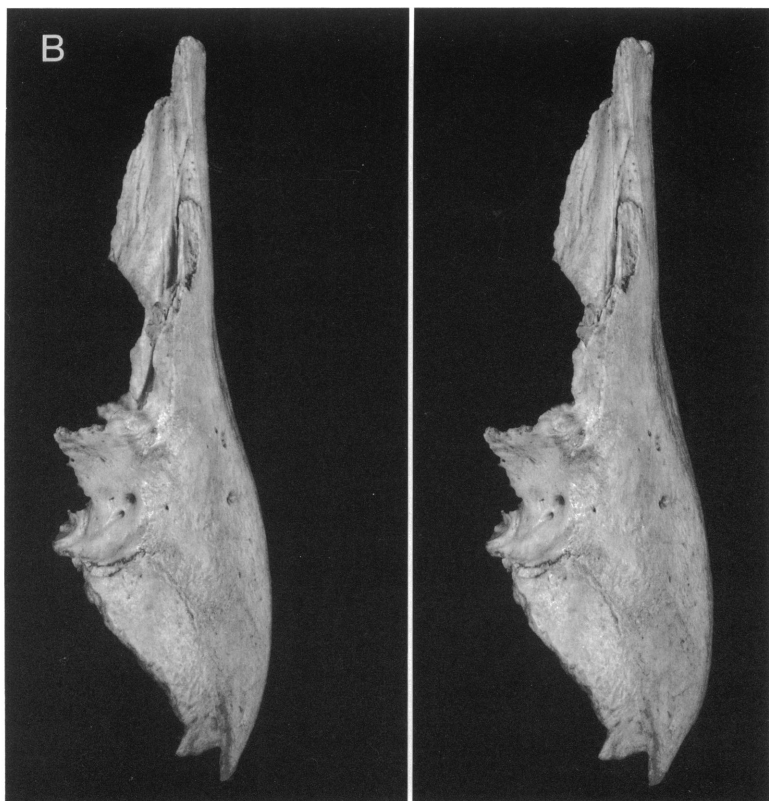


Fig. 3 (*continued*)

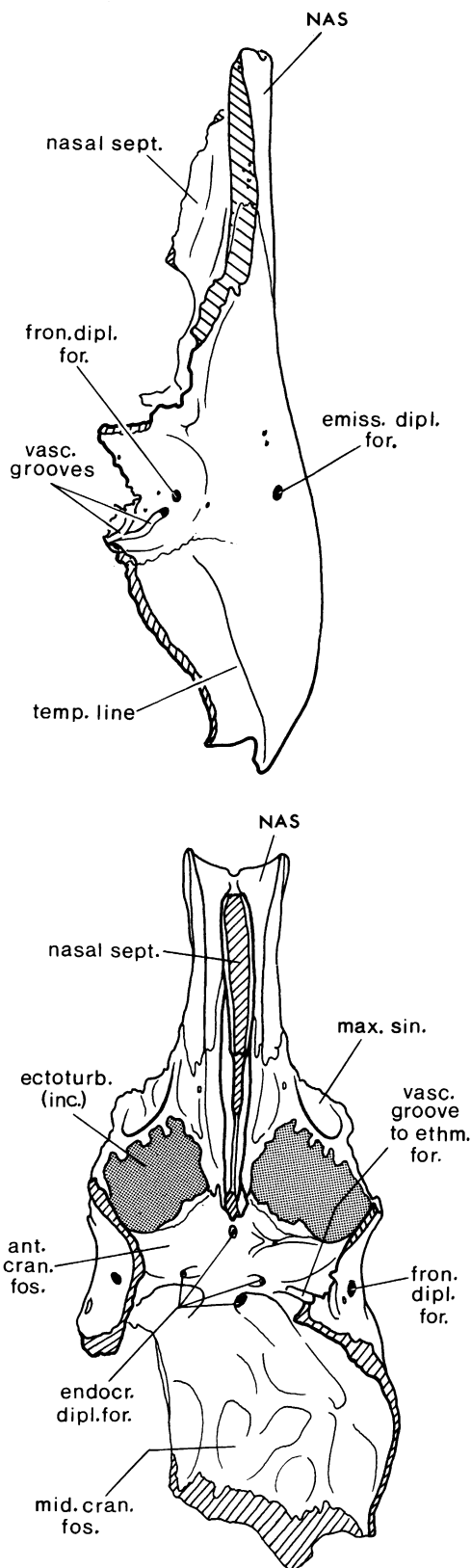


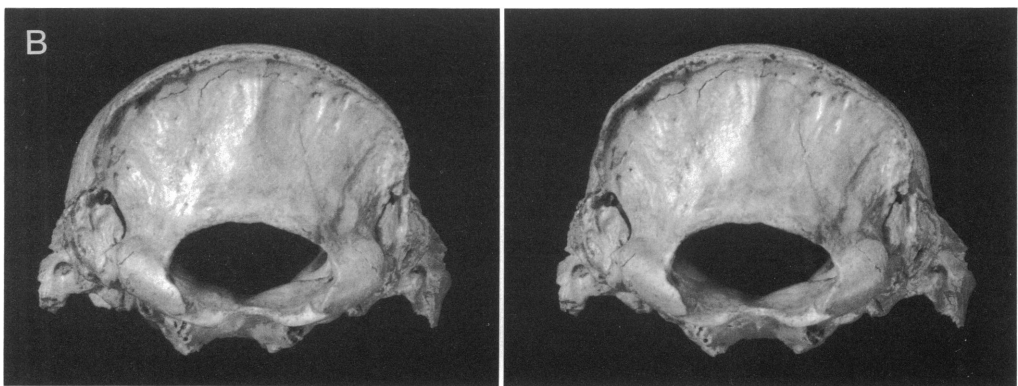
Fig. 3 (continued)

both sides; it turns outward, terminating in a tiny projection, the underside of which is deeply grooved (fig. 5C). The groove may represent the roof of a canal, although it is clearly too small to represent the roof of the infra-orbital foramen. Lamberton (1946) did not mention the presence of a foramen in this location, and it seems more probable that the groove is actually part of a sutural surface, for contact with the maxilla or possibly the jugal. Lamberton (1946: 31; cf. fig. 11A) did, however, note the existence of a small foramen in a more medial position, on a part of the anterior orbital wall that is no longer preserved. Many members of the comparative set (*Orycteropus*, *Manis*, *Tolypeutes*) have a similar aperture, on or near the frontolacrimal or palatolacrimal suture near the sphenopalatine foramen. From its position I conclude that it carries anterior ethmoidal vessels in these taxa and probably did so in *Plesiorhycteropus* as well. The outward angulation of the inferior part of the lacrimal's orbital wing (fig. 5D) may indicate that this bone participated in the formation of the root of the anterior part of the zygomatic arch, as it does in *Orycteropus*, *Dasypus*, and *Meniscotherium*.

The constitution of the anteroinferior quadrant of the orbit is not known in *Plesiorhycteropus*, although, as noted above, there is evidence that large paranasal diverticula extended into the sphenoid region of the basicranium via the cortical bone of the anterior orbital wall. In many mammals the orbital process of the frontal and the lacrimal are ventrally contacted by the palatine or, in some groups, by an enlarged orbital wing of the maxilla (Novacek, 1990). Thus in *Manis* and *Orycteropus*, this part of the orbit is formed mostly by the frontal and palatine meeting along a broad line of contact, the maxilla making very little contribution. In *Dasypus*, by contrast, the palatine lacks a significant orbital wing, and the descending process of the frontal, while large, fails to meet it. Surprisingly, it is the ethmoid and not the maxilla that fills the intervening gap. (The ethmoid contribution can easily be mistaken for an extension of the maxilla in adult animals in which most of the bones in the orbital mosaic are fused. Dissection of AMNH 133395, a young *Dasypus novemcinctus*, re-



Fig. 4. *Plesiorycteropus madagascariensis* USNMP 474080 (Anjohibe skull). Stereopair views on this and following page: **A**, dorsal; **B**, occipital; **C**, right lateral; **D**, ventral. All to scale in A. For a guide to structures, see keys for figs. 2, 3, and 5.



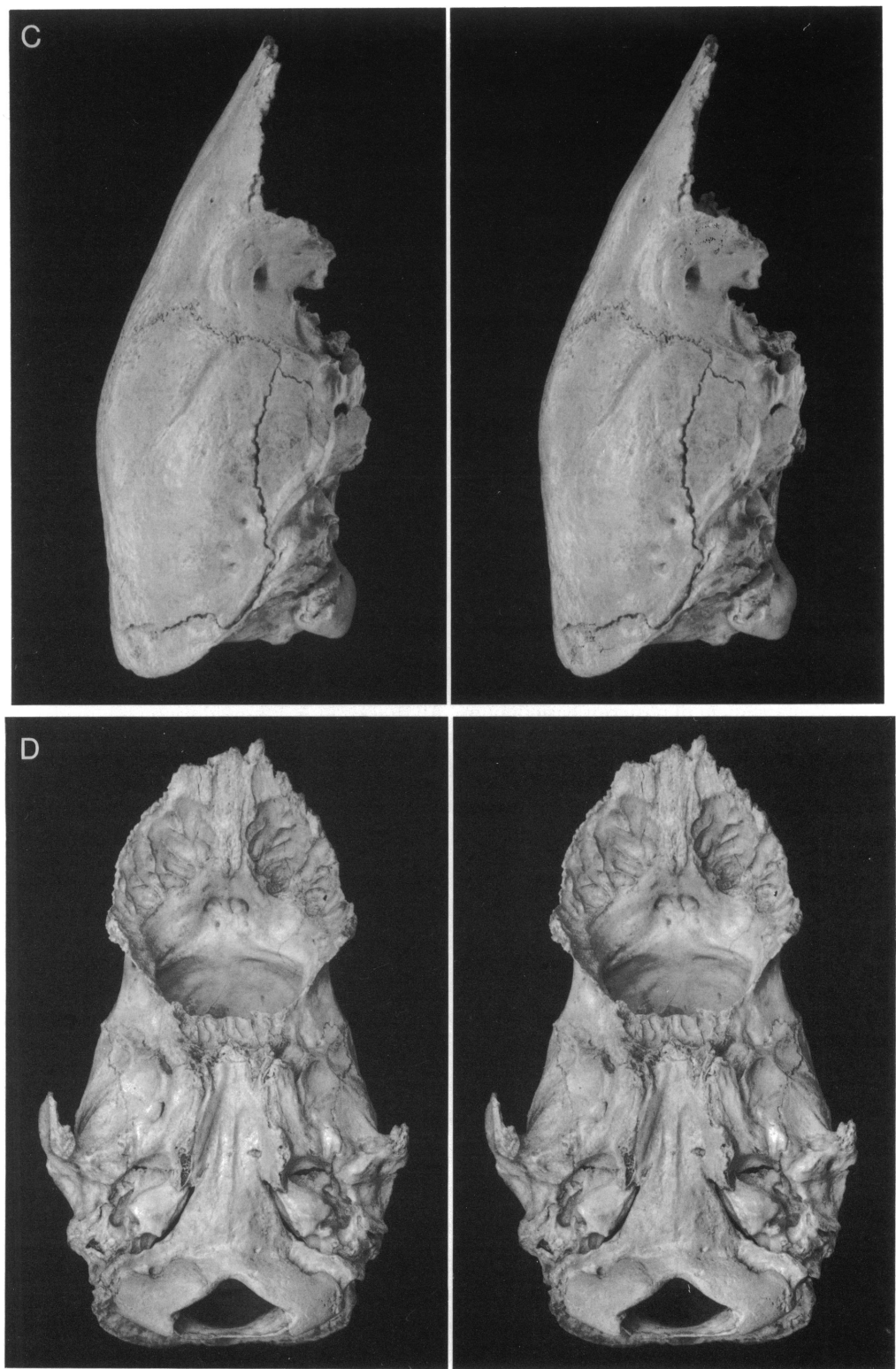


Fig. 4 (continued)



Fig. 5. *Plesiorycteropus germainepetterae* MNHNP 327, holotype (Ampasambazimba skull). Stereopair views (with keys) on this and following pages: A, dorsal; B, left lateral; C, right lateral; and D, ventral (with enlargement of posterior basicranium). All to scale in A. Ethmoid region was evidently well developed in bibymalagasy, but all that is left of it in this specimen are fragments of some turbinals and part of the perpendicular plate. Foramen magnum and occipital condyle damaged on right side. Shading in D depicts position of mandibular fossa according to Lambertson (obliques + crosshatch), Patterson (stipple), and this paper (crosshatch only). Lambertson (1946) believed that the mandibular fossa was equivalent to the entire, unevenly floored depression lying in front of the auditory region. Patterson (1975) did not accept this, arguing instead that the jaw articulated with the underside of the zygomatic process of the squamosal. Close inspection of this process as preserved in this specimen indicates that Patterson's "mandibular fossa" was not an articular surface. Lambertson's "mandibular fossa" included the area here regarded as the true mandibular fossa, but also incorporated the anterior depression interpreted as the site of origin of the lateral pterygoid muscle. Lacking a true postglenoid process, *Plesiorycteropus* must have backstopped the mandibular condyle against the pseudoglenoid process (= entoglenoid + preotic crest). The sulcus for the cartilage of the auditory tube crosses the epitympanic wing of the sphenoid (not named). Single asterisk, small foramen of unknown function situated on external border of foramen ovale; double asterisk, groove on inferior border of lacrimal; triple asterisk, bony partition subdividing spheno-orbital fissure into separate foramen rotundum and spheno-orbital foramen. In ventral view, optic canals are hidden by projecting walls of the sphenoid paranasal sinus. In right lateral view, the partition between the foramen rotundum and the spheno-orbital foramen is broken; it is intact on left.

veals that the "maxillary extension" is formed by the ethmoid [cf. Guth, 1961]. This feature is obviously variable within dasypodids, because in *Tolypeutes* the anteroinferior quadrant is floored by the maxilla.)

Caudally, the margins of the frontal, orbitosphenoid, alisphenoid, squamosal, and

parietal converge in a restricted area well behind the ethmoid foramen. The pattern of element contact is variable. In MNHNP 328, the frontal and squamosal are definitely in broad contact, to the exclusion of any contact between the parietal and the alisphenoid. By contrast, in USNMP 474080 the situation is

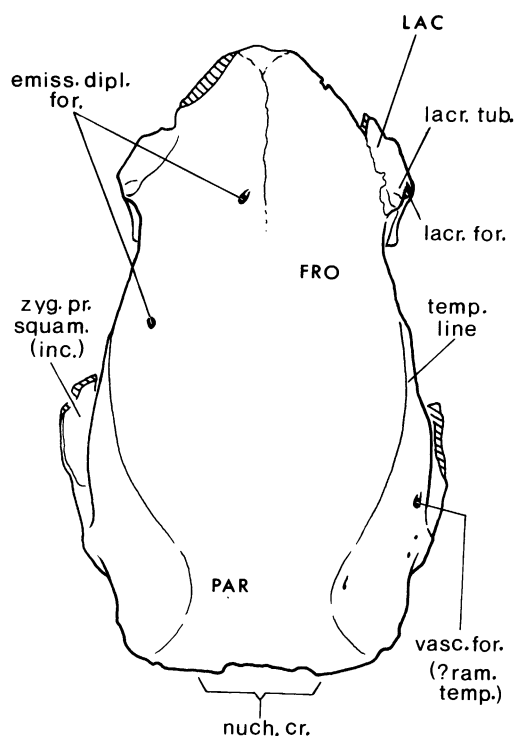


Fig. 5 (continued)

reversed: the parietal and alisphenoid are in contact, thereby excluding frontosquamosal apposition. In MNHNP 327, the situation is less clear because of sutural obliteration. However, at least on this specimen's left side, it seems that these four bones articulate in a vaguely "stellate" arrangement (fig. 5B). Since there seems to be no clear pattern of species differences between *Plesiorhycteropus madagascariensis* and *P. germainepetterae*, I do not employ the orbital mosaic in their definitions (see Material, Occurrence, and Taxonomy).

The caudal limit of the orbit is frequently difficult to define in mammals lacking post-orbital processes of the frontal. Manids, myrmecophagids, and dasypodids lack distinct postorbital processes, but usually possess a raised, roughened area (lower down on the orbital wall than where a postorbital process would be located) that I assume marks the point of attachment of the temporalis fascia. *Plesiorhycteropus germainepetterae* MNHNP 327 has a well-defined temporal tubercle high on the skull, on the frontoparietal suture (fig.

5B, C). This eminence is barely indicated on the skulls assigned to *P. madagascariensis* (figs. 2D, 4C), which I interpret as a species difference.

FORAMINA OF ORBIT

Although Thewissen (1985) corrected errors made by Lamberton (1946) and Patterson (1975) in identifying the contents of foramina exposed on the walls of the orbits in bibymalagasy, his account contains some discrepancies which I will try to resolve here.

The lower half of the bibymalagasy orbital region exhibits a suite of closely spaced foramina, set out along a moderate incline. In the available complement of specimens these foramina are variably preserved, and only one of them (MNHNP 327, fig. 7) preserves the complete set. This situation has produced conflicting interpretations of the contents and homologies of these apertures. As demonstrated below, the interpretation most consistent with the anatomical facts is that these foramina (viewed from ventral to dorsal) correspond to foramen rotundum, speno-orbital foramen, optic canal, and (posterior) ethmoid foramen.

Because the homologies of these foramina in bibymalagasy have been variously interpreted by other workers, it is useful to begin with some definitions relating to the name and position of apertures for the sensory divisions of the fifth (trigeminal) cranial nerve. It is thought to be primitive for eutherians (cf. Novacek, 1986, 1993b) to transmit the ophthalmic (V1) and maxillary (V2) divisions of the fifth cranial nerve through a single aperture, the speno-orbital (rotundo-orbital) fissure, in company with cranial nerves III, IV, and VI. In some mammals (e.g., *Homo*; Warwick and Williams, 1973), the speno-orbital fissure becomes subdivided during early ontogeny by a strut derived from the ala temporalis or its ossified successor, the alisphenoid. In these cases, the speno-orbital fissure yields two daughter foramina, the speno-orbital foramen (for V1, III, IV, and VI) and foramen rotundum (for V2 only; C 7). Arteries and veins are also transmitted by these ports.

MNHNP 327 exhibits a large, almost circular aperture in advance of foramen ovale

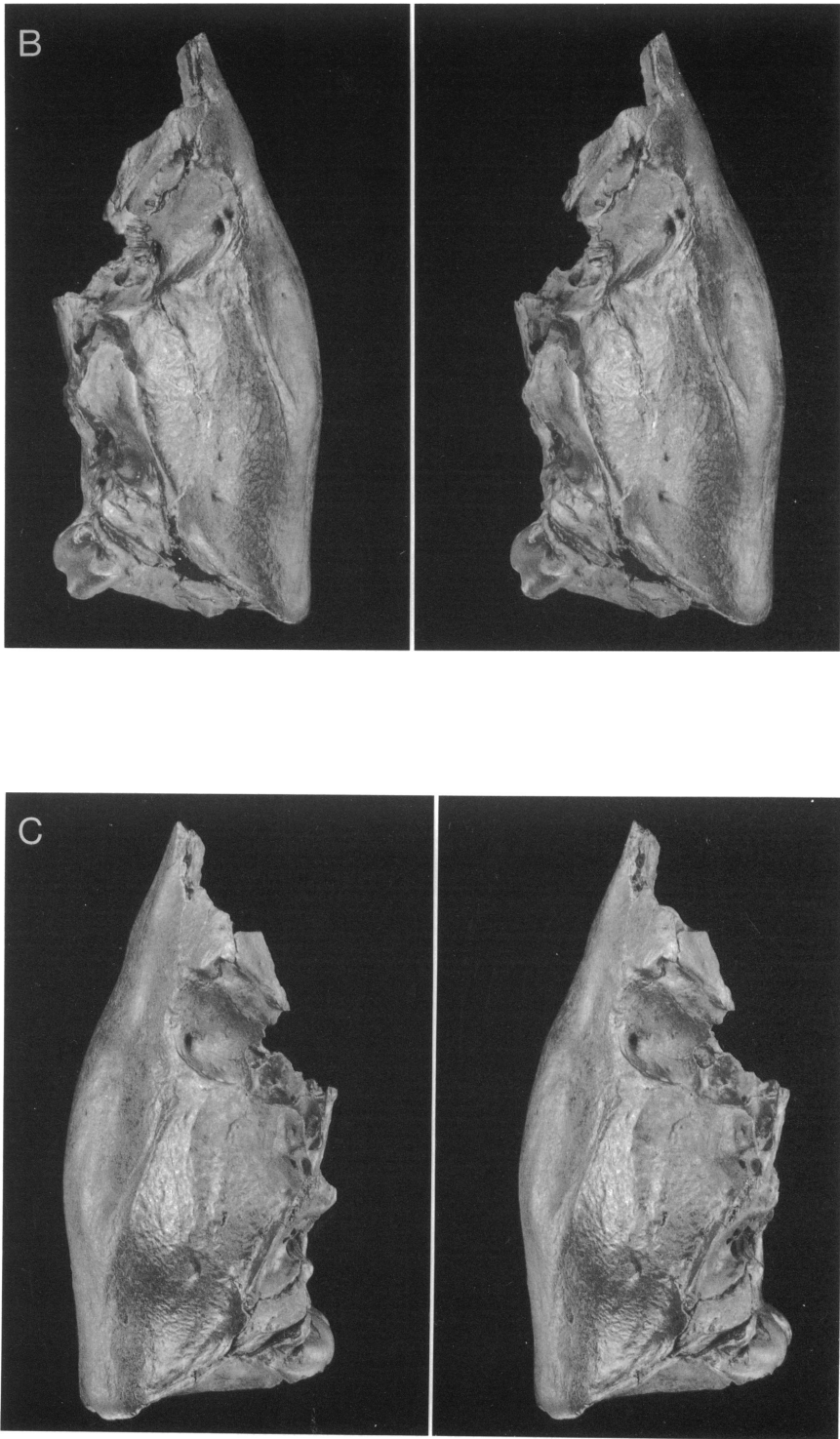


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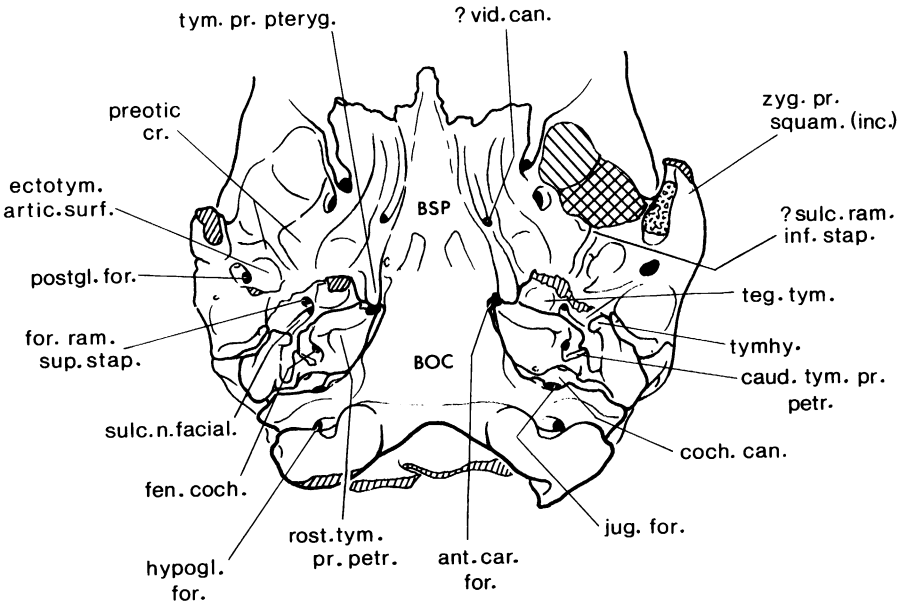
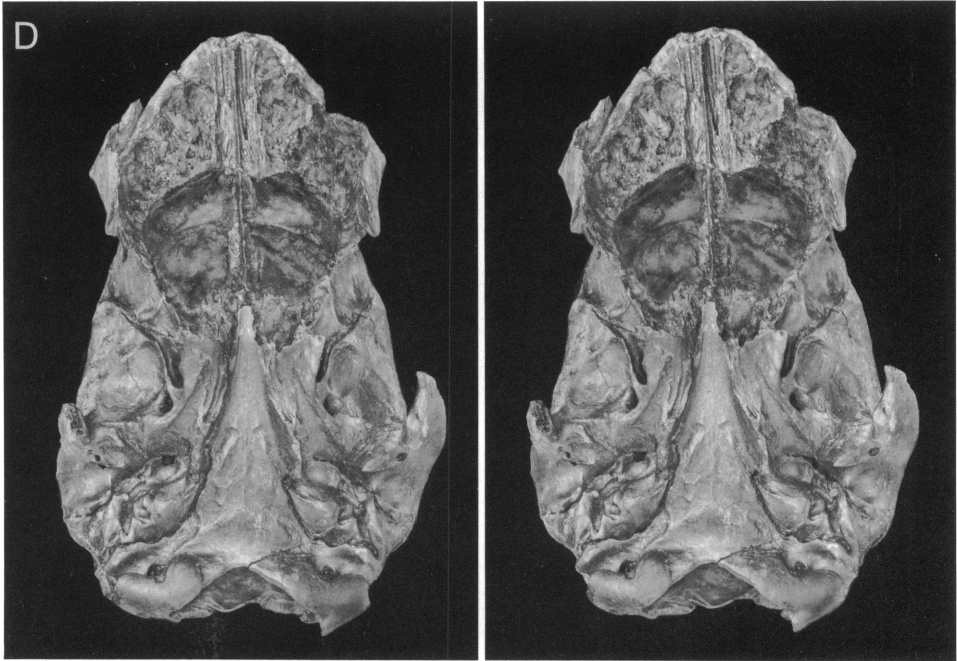


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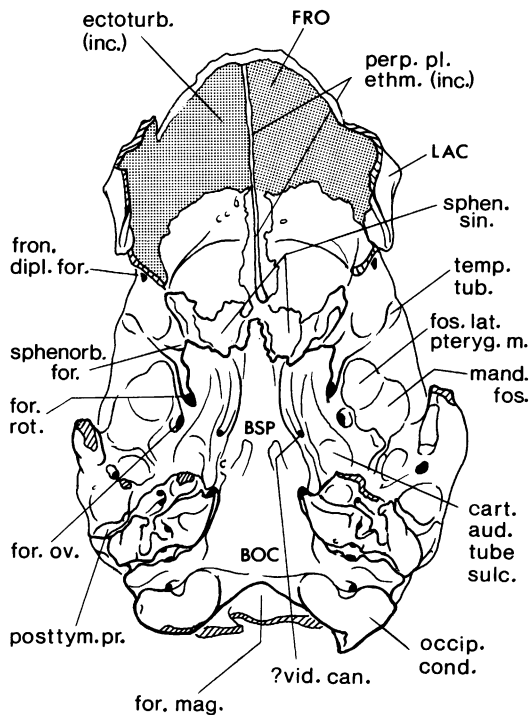


Fig. 5 (continued)

I infer that foraminal organization in *P. madagascariensis* was similar in all pertinent respects. If there is a consistent species difference, it will have to be demonstrated on the basis of better material.

The aperture that I regard as foramen rotundum is much larger than either foramen ovale or the sphenoidal foramen, which tends to suggest that the sensory input from the divisions of the maxillary nerve was correspondingly large. In the absence of soft-tissue evidence, the size of foramen rotundum cannot be correlated with any single structure in the maxillary field of supply, such as unusually large sensory projections from mystacial vibrissae. According to Novacek (1986), foramen rotundum as a discrete aperture is derivedly present in xenarthrans, scandentians, euprimates, and pholidotans (but there are major exceptions within most of these groups; see also Zeller [1989] and Novacek [1993b]). Ungulates are variable (C 7).

As Thewissen (1985) conclusively demonstrated on the basis of endocast features,

in *Plesiorhycteropus* the optic nerve passed out of the endocranium through the relatively tiny, upwardly directed channel in the orbitosphenoid that lies above the "slit-like" sphenoidal foramen (fig. 7). Lamberton (1946) incorrectly stated that the channel was for cranial nerves III and IV; an aperture is illustrated but not identified in his figure, reproduced here as figure 11A. In the three bibymalagasy skulls with the relevant region preserved, the optic canals are approximately 1 mm in diameter, which is comparable to the width of the optic canals in *Solenodon*, a much smaller animal (fig. 8). In MNHN 327, the optic canals are among the smallest apertures on the orbital wall, being as small as or smaller than the frontal diploic foramina (fig. 5B, C). These facts strongly suggest that *Plesiorhycteropus* was micro-ophthalmic (C 1). The homology of the tiny vascular foramen (?suboptic foramen) situated immediately ventral to the optic canal (easily seen in fig. 5B) has not been established.

Of the major foramina in the orbital wall, by far the largest is the (posterior) ethmoid foramen, which is framed by the orbital process of the frontal and the dorsal part of the orbitosphenoid. In eutherians this aperture typically conducts the ethmoid artery, vein, and nerve (cf. Thewissen, 1985; Prince et al., 1960), and is an extremely common feature of the orbital sidewall. This aperture is no longer complete on any of the available skulls, although it is depicted with intact margins in Lamberton's (1946) schematic drawing of the bibymalagasy orbit (fig. 11A, feature f). Intracranially, it can be seen that each ethmoid foramen lies at one end of major endocranial vascular grooves that run around the periphery of the cribriform plate (fig. 3C).

As Thewissen (1985) noted, the ethmoid foramen is much larger in *Plesiorhycteropus* than in *Orycteropus*. It is also larger than in any extant member of the comparative set, including lipotyphlans (fig. 6). The size of the ethmoid foramen is difficult to ascertain in the fossil ungulates, but seems to be relatively small where known (e.g., *Phenacodus*, *Mensicotherium*, *Pleurospirotherium*). Lamberton (1946: 31), who believed that the hole was too large to be an exclusively vascular port, considered the possibility that it was an

orbital fenestration, i.e., a persistently unossified part of the skull, probably mostly filled with cartilage in the living animal. I regard this interpretation as quite unlikely.

Incising the rear margin of the ethmoid foramina of bibymalagasy are deep grooves, interpreted as vascular (e.g., figs. 2D, 7). Lamberton (1946: 31) stated that in *Plesiorhycteropus* the large grooves terminated in a medium-sized aperture near the suture between the frontal and the alisphenoid, which suggests the presence of a cranio-orbital foramen (for transmission of the sinus vein and, I suggest, the ramus superior of the stapedia artery). A foramen, much smaller than the aforementioned grooves, can be made out in this location in USNMP 474080 and MNHNP 327; in MNHNP 328, the position of the foramen has to be inferred because the suture has sprung open.

In *Plesiorhycteropus*, the deep groove gives off smaller channels that run up the sidewall of the orbit to small accessory foramina near the summit of the orbit. Bristles passed through the larger foramina enter long canals that travel dorsomedially, to open near the midsagittal plane on the endocranial side of the cranial roof (fig. 3B, C). I assume that the smaller foramina, which could not be probed, are exit-points for canals that either terminate in the diploe or anastomose with the larger canals. The position and relations of the large canals indicate that they are best interpreted as channels for frontal diploic veins that not only drained the cranial diploe but also communicated with the superior sagittal cerebral sinus (Thewissen, 1985; for a comparative anatomy of these veins, consult Thewissen, 1989). In general, frontal diploic veins drain into the veins of the orbit, and are thus important collateral channels for endocranial venous drainage ancillary to the internal jugular system.

The simplest interpretation of these anatomical features—frontal diploic foramina, ethmoid foramen, prominent vascular grooves in orbital wall—is that they relate to a large drainage complex in the dorsal and posterior parts of the orbit. This complex apparently involved venous return not only from the nasal cavity but also from the anterior parts of the brain and meninges. Because there would be little functional point in bringing

venous blood from these areas into the orbit only to send it back into the braincase via ophthalmic veins, it is reasonable to believe that the blood was probably carried away via anastomoses between the ophthalmic and facial veins.

It is of course possible that the large ethmoid foramen also transmitted a sizeable ethmoid artery in addition to veins. The ethmoid artery, a division of the so-called “external” ophthalmic artery, is normally a small vessel, with a supply area limited to the mucous membrane covering the cribriform plate, the posterior parts of the nasal capsule, and a small portion of the dura mater (Ellenberger and Baum, 1908). In a few mammals it has a greater significance, actually supplying blood to the rostral end of the circulus arteriosus. In cavioids with this arrangement (cf. Bugge, 1974), the importance of the “external” ophthalmic for cerebral and dural supply is correlated with the obliteration of the internal carotid, proximal stapedia, and ramus superior. These correlations obviously do not apply to *Plesiorhycteropus*, and this fact makes it unlikely that the ethmoid artery played a substantial role in brain supply.

Among members of the comparative set, a pronounced groove emanating from the posterior side of the ethmoid foramen may be seen in *Orycteropus*, *Dasypus*, and *Prodonates* (fig. 6). Thewissen (1990) described an arrangement for *Phenacodus intermedius* in which grooves emanate from the frontal diploic foramen (probably equivalent to the ethmoid foramen of this paper).

INFRATEMPORAL FOSSA AND CRANIOMANDIBULAR JOINT

INFRATEMPORAL FOSSA

The shape of the infratemporal fossa cannot be accurately determined because of bone loss, but I infer from the position and orientation of the stub of the zygomatic process of the squamosal in MNHNP 327 and USNMP 474080 that the posterior part of the fossa was transversely narrow (arch to sidewall of skull). Together with the low temporal lines, the narrowness of the fossa implies, but does not prove, that the temporalis musculature was comparatively small.

In MNHNP 327, but not in the skulls as-

signed to *P. madagascariensis*, there is a small foramen that dorsally flanks the much larger foramen ovale (figs. 2–5, 7). However, a groove can be made out just above foramen ovale in the skulls of *P. madagascariensis* (deeply incised only in USNMP 474080), and I infer that it accommodates the structure—presumably a vessel—that perforates the foramen seen in MNHNP 327. (There is no basis for assuming that this aperture is a buccinator or masseteric foramen.) Because the unnamed foramen is situated on the dorso-lateral rather than the medioventral side of foramen ovale, I consider it unlikely that it gave passage to a homolog of the “middle meningeal” branch (= ramus anastomoticus) of the maxillary artery (see MacPhee and Cartmill, 1986; Wible, 1987). By elimination, this leaves the interpretation that the foramen was a venous port. The foramen is unlikely to be a true transverse sinus canal because it does not appear to be part of a channel running through the central stem to provide drainage for the cavernous sinus. Moreover, the true transverse sinus canal is always located on the medial or rostromedial side of foramen ovale (cf. many marsupials, dasypodids, *Solenodon*, and *Orycteropus*), not lateral to it. Thewissen (1990) reported the presence of small foramina near foramen ovale in one specimen of *Phenacodus intermedius*, but did not interpret their function.

CRANIOMANDIBULAR JOINT

Usually, identification of the position of the craniomandibular joint in a mammal is a straightforward matter. Lamberton (1946) and Patterson (1975), however, reached sharply different conclusions about the location of the mandibular fossa in *Plesiorhycteropus*. According to Lamberton (1946: 30), the mandibular fossa conforms to the very large, shallow excavation on the sidewall of the skull that extends from the anterior wall of the middle ear to the posterolateral limit of the speno-orbital foramen (fig. 11B). The long axis of this depression is approximately 10.5 mm—large indeed for an animal the size of *Plesiorhycteropus*—and it does not impinge on the zygomatic arch at all. Lamberton (1946) noted that the mandibular fossa was divided into anterior and posterior parts by

a slight ridge, but evidently considered the whole complex to be for the reception of the jaw's condyle.

Patterson (1975: 212) rejected this interpretation. He located the mandibular fossa on the ventral margin of the blade-like zygomatic process of the squamosal (his “glenoid process”; see fig. 10B, C), describing it as “an elongate, narrow, transversely convex and poorly defined articular surface,” held away from the sidewall of the skull as in pangolins. Because of its position, he argued, the jaw articulation would have been low relative to the basicranial planum. Patterson agreed with Lamberton that a (true) postglenoid process was absent.

Both Lamberton (1946) and Patterson (1975) described the morphology of the mandibular fossa in terms that imply strong contrasts with *Orycteropus*. The aardvark's moderately deep mandibular fossa is located high up on the skull, dorsolateral to the auditory region, and is backed by a large postglenoid process (fig. 8). In addition, its surface impinges on the underside of the zygomatic process as well as the sidewall of the skull, which is the typical condition for eutherian mandibular fossae. Lamberton (1946) did not discuss structural contrasts between bibymalagasy and aardvark jaw joints, noting only that the comparatively short transverse distance between the mandibular fossae in *Plesiorhycteropus* suggested a narrow, elongated mandible, as in tubulidentates. Patterson (1975) offered a more complex analysis that sought to explain the apparently sharp contrast between *Orycteropus* and *Plesiorhycteropus* as a consequence of the latter's complete morphological commitment to myrmecophagy. Patterson speculated that this commitment was probably correlated with edentulousness and severe reduction of the mandible, as in pangolins and myrmecophagids.

Having examined both authors' interpretations and the evidence cited for each, I have concluded that both made errors in describing the position and nature of the mandibular fossa. We may consider Patterson's (1975) evidence first.

MNHNP 327 must be the skull on which Patterson based his interpretation of jaw joint position. In this specimen, the area that Patterson identified as articular has a maximum

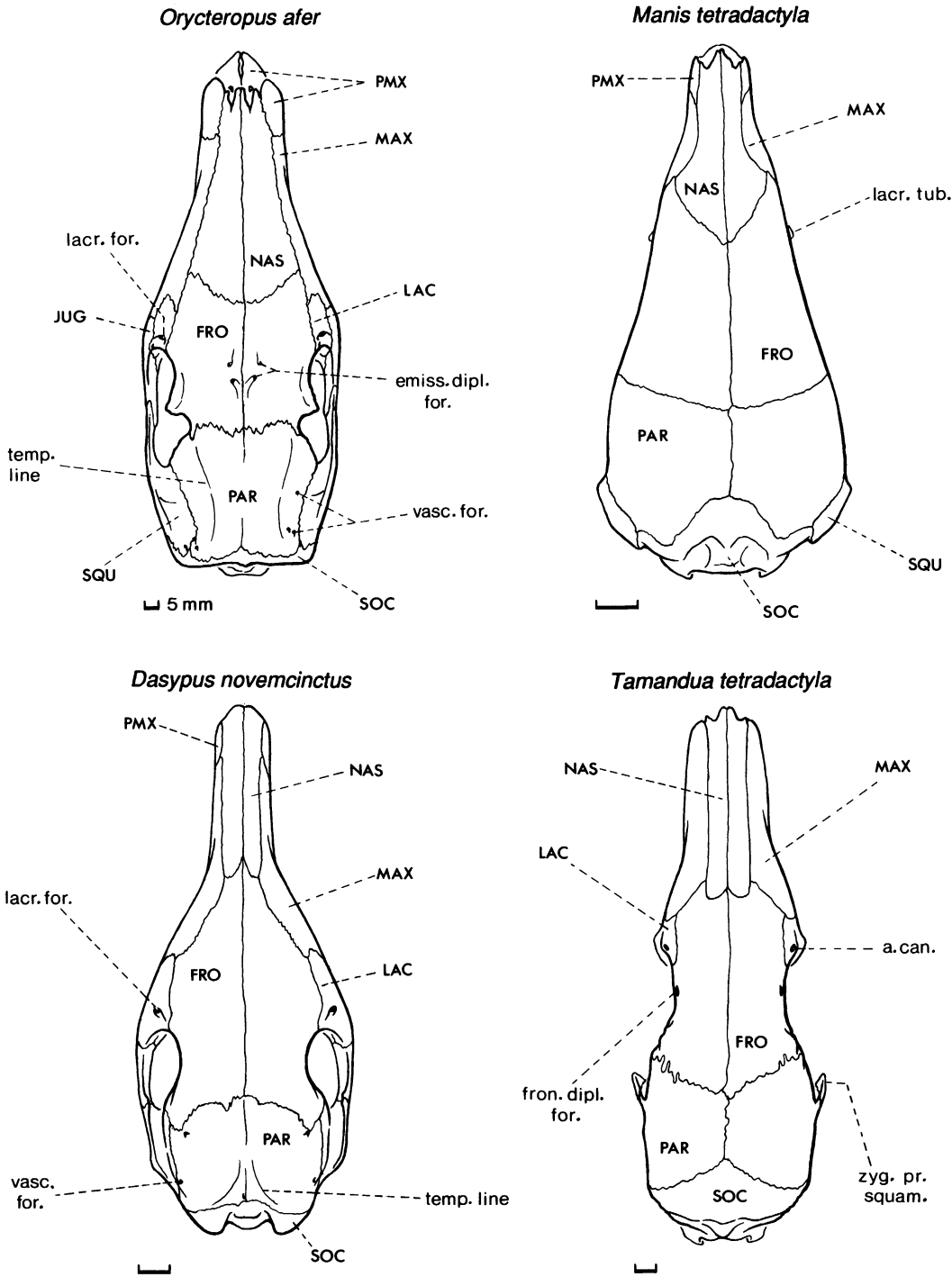


Fig. 6. Cranial morphology of representative members of comparative set (see table 5), as seen from dorsal, left lateral, ventral, and occipital aspects. All drawn to same rostrocaudal length; all scales 5 mm.

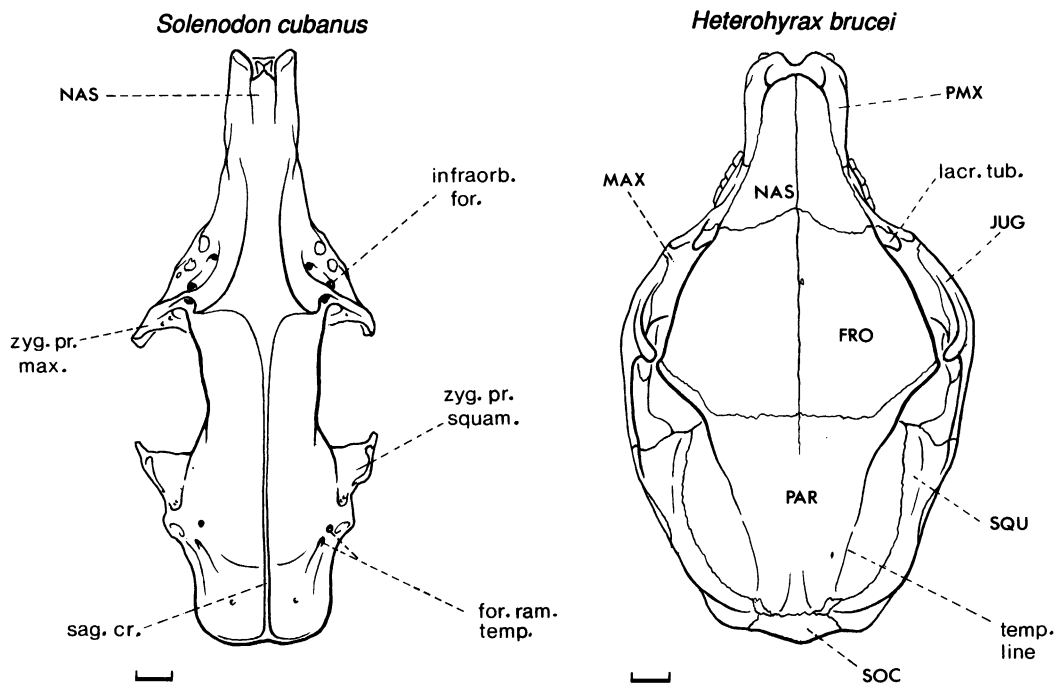


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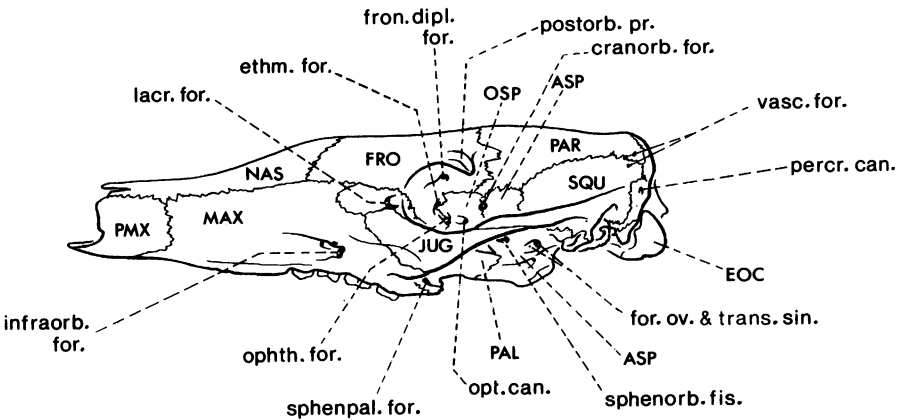
ventral width of approximately 2 mm and appears to be completely intact posterior to the place of obvious fracture seen in figure 5D. Rather than being smoothly convex, however, the relevant area has a cobbly, uneven appearance, and is centrally pierced by a substantial nutrient foramen. There is nothing here that, in my view, could be reasonably interpreted as an articular facet for the head of the mandible. Moreover, the ventral surface as a whole is inclined ventrolaterally, not directly ventrally as Patterson (1975) stated. By contrast, in manids the squamosal articular surface for the mandibular condyle is clearly set off from surrounding areas by the orientation and texture of the bone that forms it (fig. 8). In pangolins the glenoid is smooth and inwardly facing, and nutrient foramina on the articular surface are mere pinholes. These observations also apply to the more typically-positioned mandibular fossae of myrmecophagids (fig. 8).

If Patterson's interpretation of the position of the mandibular fossa is untenable, what of Lambertson's? It was previously noted that

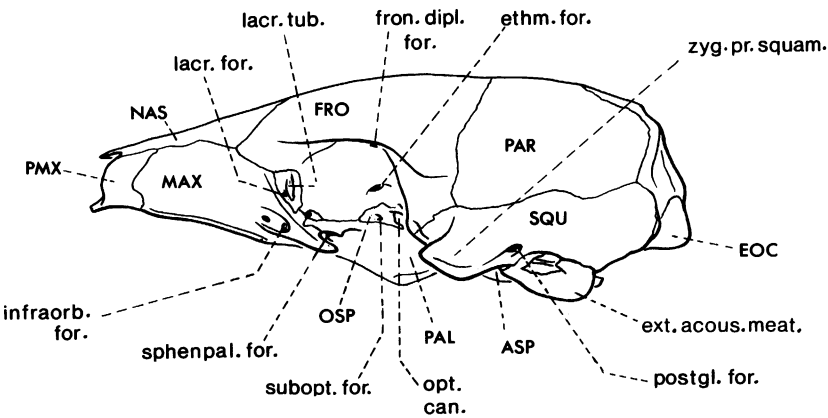
the area which Lambertson described as the mandibular fossa appears to be divisible into two parts. On close examination of MNHNP 327 and the other skulls, I found that the anterior part of the fossa as defined by Lambertson has an undulating, uneven surface. By contrast, the posterior part is smoother and thus more closely resembles a typical articular surface. The smooth area continues for a short distance onto the ventromedial aspect of the "notch" at the root of the zygomatic arch. This area is bounded posteromedially by a low eminence through which the suture between the alisphenoid and entoglenoid part of the squamosal runs. In MNHNP 328, these rough and smooth areas can be easily distinguished (fig. 9A). Of particular note is the fact that the smooth area is delimited by a wreath of small pits and a fine arcuate line, highly suggestive of the attachment site of a joint capsule. USNMP 474080 retains only the stumps of each zygomatic process and thus adds nothing to what may be gleaned from previously investigated specimens.

These findings support the following inter-

Orycteropus afer



Manis tetradactyla



Dasypus novemcinctus

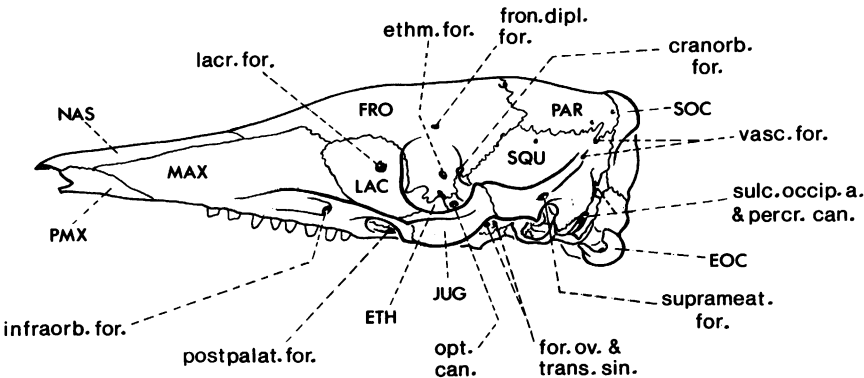
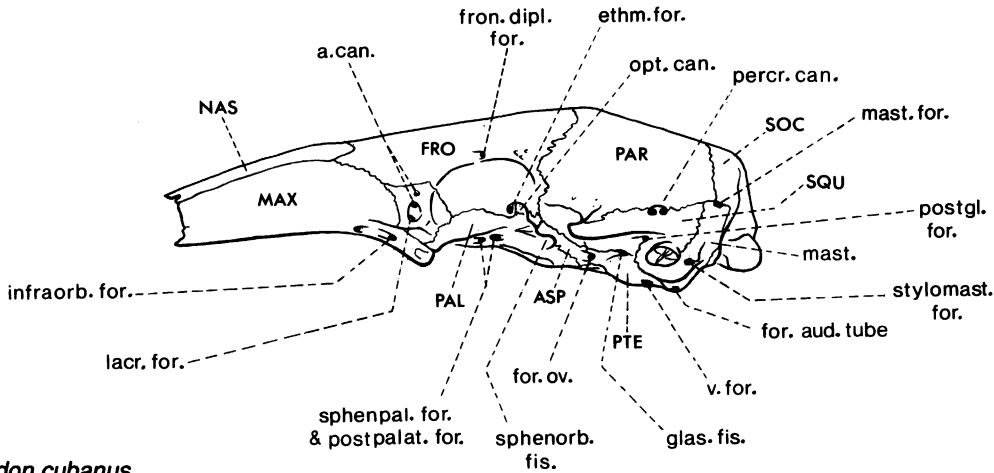
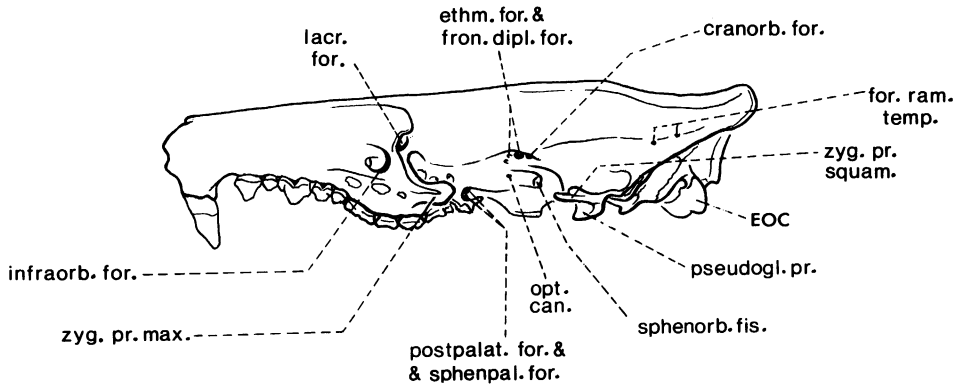


Fig. 6 (continued)

Tamandua tetradactyla



Solenodon cubanus



Heterohyrax brucei

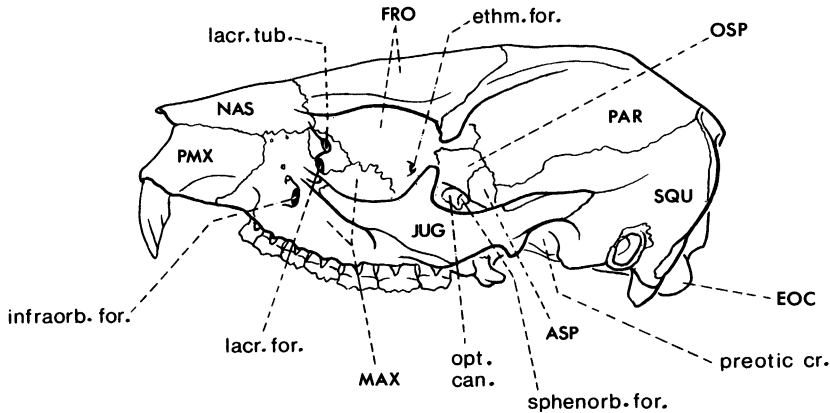
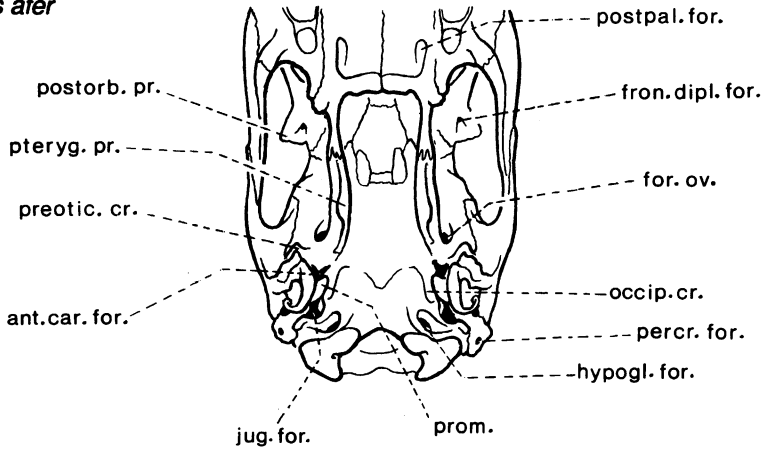
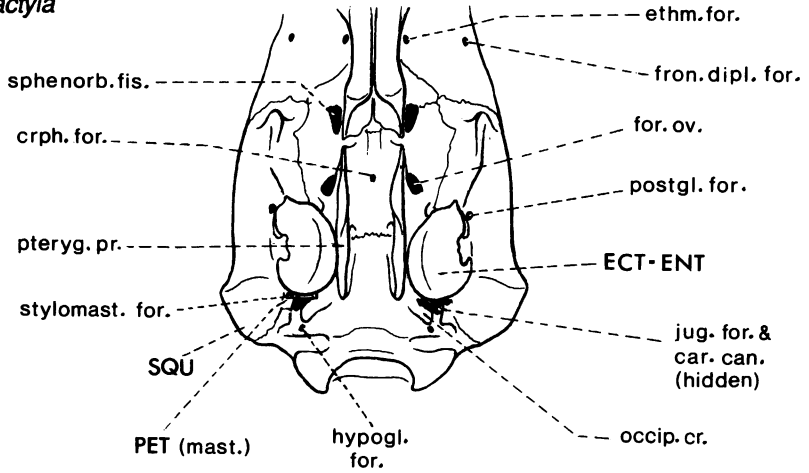


Fig. 6 (continued)

Orycteropus afer



Manis tetradactyla



Dasypus novemcinctus

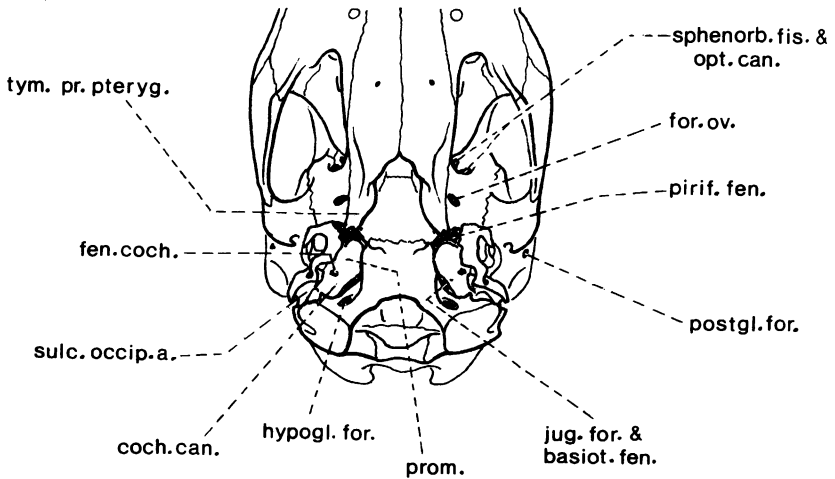
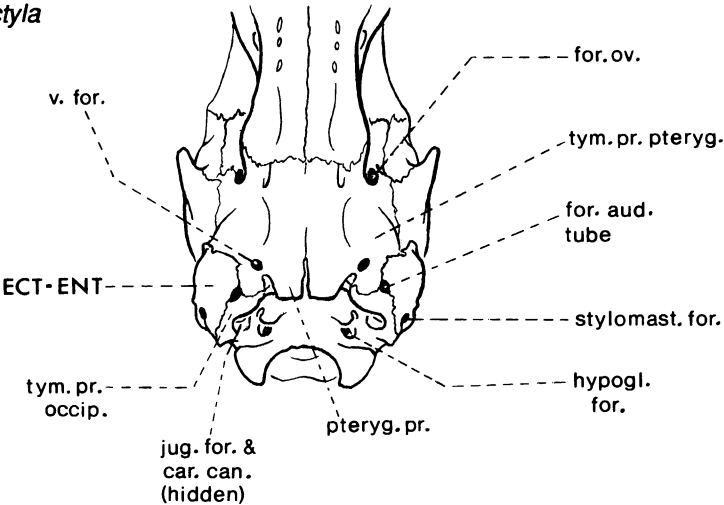
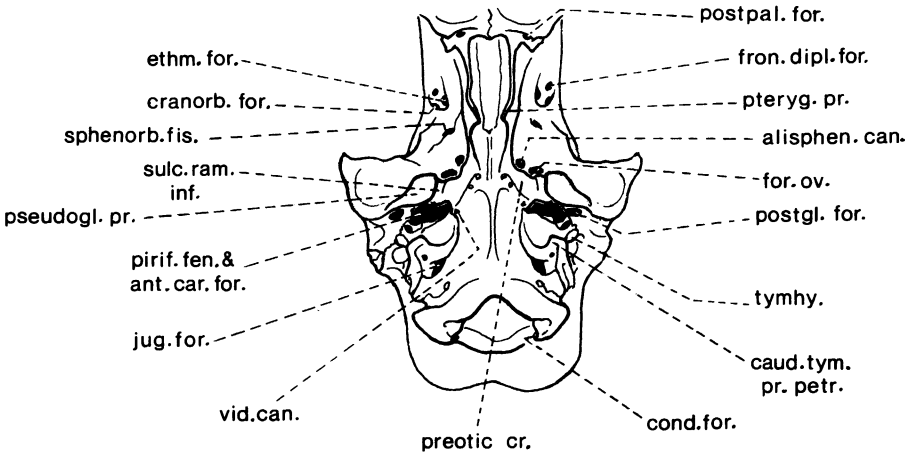


Fig. 6 (continued)

Tamandua tetradactyla



Solenodon cubanus



Heterohyrax brucei

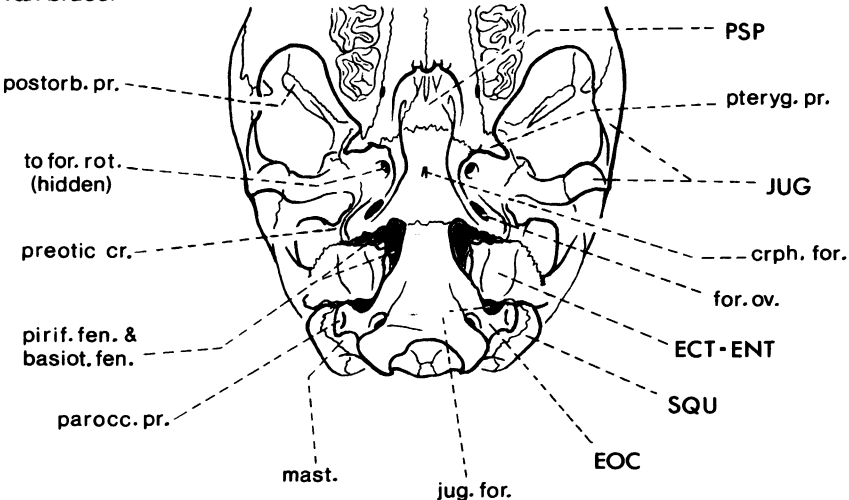
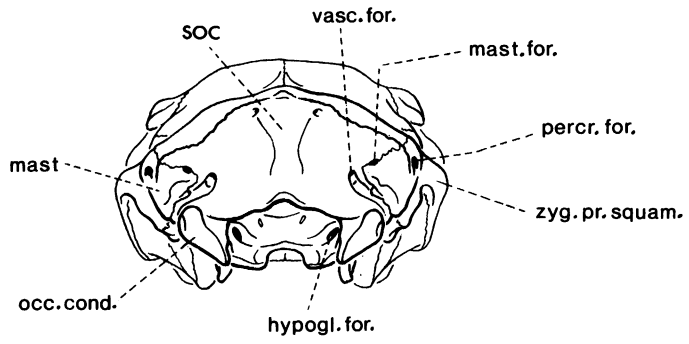
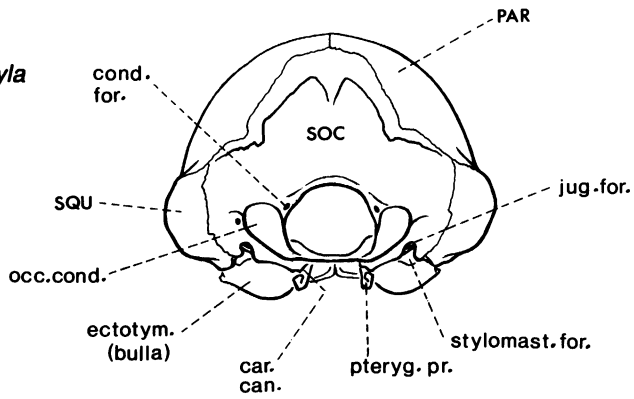


Fig. 6 (continued)

Orycteropus afer



Manis tetradactyla



Dasypus novemcinctus

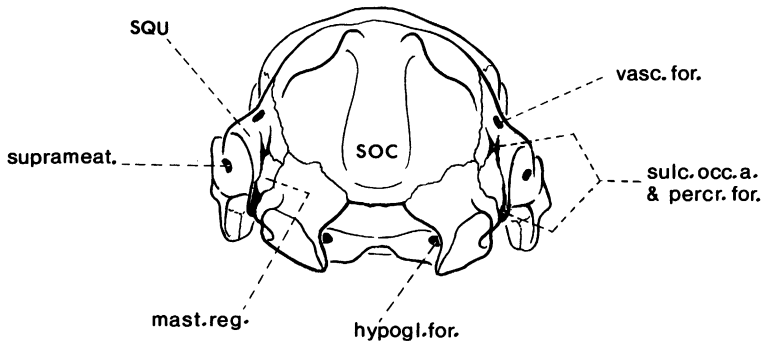
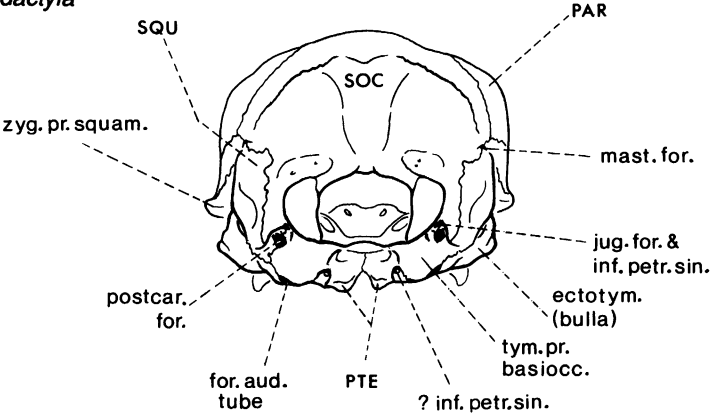
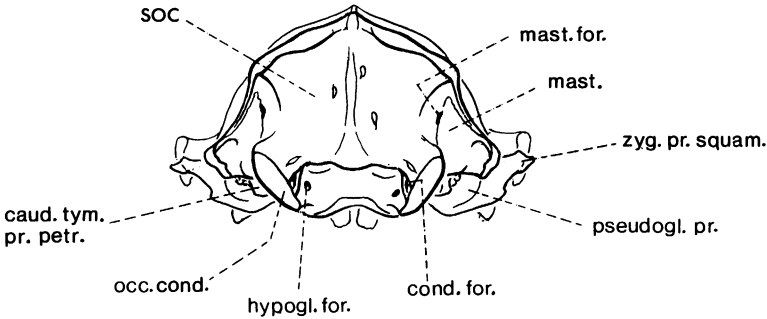


Fig. 6 (continued)

Tamandua tetradactyla



Solenodon cubanus



Heterohyrax brucei

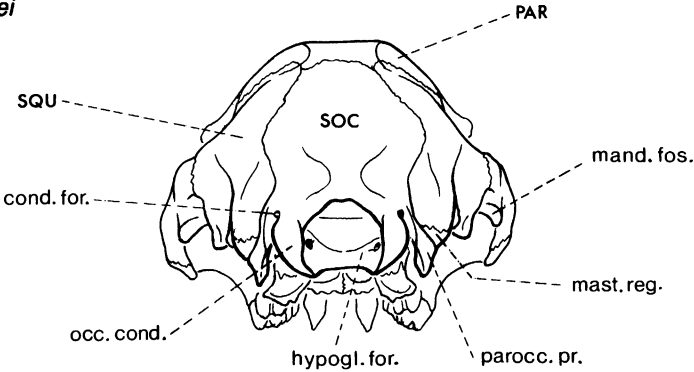


Fig. 6 (continued)

pretations regarding the position and nature of the mandibular fossa in *Plesiorcyteropus*: (1) The shallow, smooth-surfaced fossa approximately 4 mm long that lies rostromedial to the root of the zygomatic arch of the squamosal is in the correct position to be, and is here interpreted as, the true mandibular fossa. (2) The rough texture of the bone lining the other fossa suggests that this excavation provided an attachment site for a muscle (here assumed to be the lateral pterygoid). (3) The raised eminence seen in MNHNP 328 and USNMP 474080 (damaged in MNHNP 327) conforms to a pseudoglenoid process, wholly formed by the preotic crest (for definition, see McDowell, 1958); it is in the correct position to act as a backstop for a mandibular condyle seated in the mandibular fossa lying in front of it. (4) The smooth area on the inner aspect of the root of the zygomatic process of the squamosal, if real, is probably a continuation of the craniomandibular joint surface onto the root of the zygomatic arch. (5) The underside of the zygomatic arch does not appear to have been a joint surface; it may have functioned as a site of muscle or ligament attachment, or perhaps for sutural articulation with another bone, presumably the jugal.

This reinterpretation of the position and form of the mandibular fossa does not solve all morphological problems. As defined here, the craniomandibular joint of *Plesiorcyteropus* was restricted almost completely to the sidewall of the neurocranium (i.e., it did not significantly encroach onto the zygomatic process of the squamosal). This is a rare but not unprecedented condition. In many rodents (e.g., murids), the mandibular fossa barely invades the zygomatic arch, although in other respects conditions are completely different. (Mandibular fossae of rodents are anteroposteriorly elongated and transversely concave, set well above the level of the auditory region, and not backed by a glenoid or pseudoglenoid process.) In golden moles, the deeply concave mandibular fossa is separated by a distinct gap from the root of the zygomatic arch, but once again conditions are otherwise quite unlike those encountered in bibymalagasy. There are vague resemblances to tenrecids, soricids, and hyraxes in the modification of the entoglenoid to clasp the

dentary, although on the whole jaw joint organization in bibymalagasy is not very much like that of any known mammal.

For completeness, I will note that the surface identified as the dorsal wall of the external acoustic meatus could not have been the site of the craniomandibular joint. Sufficient reasons for rejecting this possibility are the anomalous position of the "articular" surface (posterior to the postglenoid foramen and probable track of the chorda tympani) and its relationship to the tympanic cavity (lateral pterygoid muscle would have to pass through the tympanic membrane in order to attach to the mandibular head).

Patterson (1975) placed much emphasis on the "lowered" position of the craniomandibular joint in *Plesiorcyteropus* as a feature diagnostic of myrmecophagy. Although my interpretation of the position of the jaw joint places it at or slightly above the horizontal plane of the external acoustic meatus, the functional implications are practically the same. The small area and shallow depth of the mandibular fossa, combined with the absence of a significant condylar backstop, are incompatible with powerful biting or shearing.

BASICRANIUM

Lamberton (1946) did not provide a detailed description of the bibymalagasy basicranium, and Patterson (1975) almost ignored it. Thewissen's (1985) contribution was mainly concerned with vascular features, and contains a few errors or arguable interpretations that need to be reconsidered.

BASICRANIAL KEEL

The bones that form the basicranial keel—the exoccipitals, basioccipital, basisphenoid, and presphenoid—are thoroughly fused in available specimens, and no special features mark their synchondroses. The synchondrosis that originally separated the basisphenoid and presphenoid was probably situated near the craniopharyngeal foramen (for the hypophyseal stalk), still patent in MNHNP 328 (fig. 2C). A noteworthy feature is that the keel is broad through the exoccipitals, but narrows rapidly in the rostral direction in both species of *Plesiorcyteropus*.

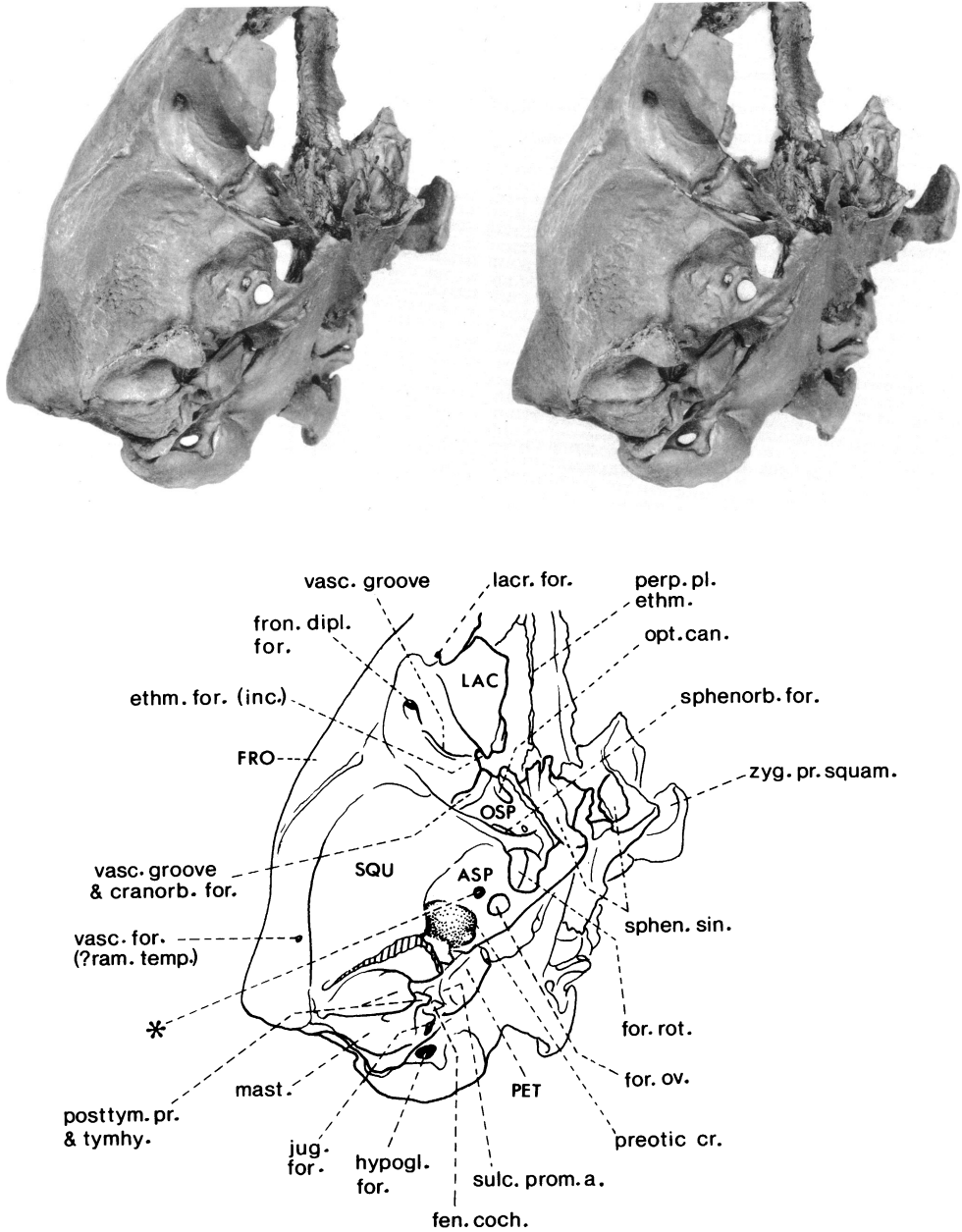


Fig. 7. Oblique lateral view of *Plesiorycteropus germainepetterae* MNHNP 327 (Ampasambazimba skull), showing details of orbital and infratemporal regions (stereopair, with key). Approximately to same scale as fig. 5. The region of the mandibular fossa is stippled (cf. fig. 8). Asterisk, foramen of unknown function on dorsal margin of foramen ovale.

The pterygopharyngeal region constitutes the anterior portion of the basicranium, in advance of the basioccipital-basisphenoidal synchondrosis. In mammals, this area is typ-

ically delimited laterally by the pterygoid laminae and anteriorly by the nasal choanae. This region is largely intact in three of the four bibymalagasy skulls. The choanae them-

selves are not represented in the available material, but presumably lay immediately in front of the broken remnants of the sphenoid paranasal sinus. Marked posterior elongation of the choanae, as seen in myrmecophagids and manids, is obviously absent in the Malagasy subfossil.

In MNHNP 327 (fig. 5D), as in the other bibymalagasy skulls, the interpterygoid region is a broad gutter that extends posteriorly to the auditory region. Precise contributions to the walls of the gutter cannot be discriminated because of sutural fusion, but it is reasonably clear that they are largely built from the massively inflated anterior parts of the sphenoid, especially the pterygoids and the medial portions of the orbitosphenoids and alisphenoids. Pterygoid laminae are merely suggested by weak ridges. The lateral pterygoid lamina (ectopterygoid) may be considered absent. The medial lamina becomes more prominent caudally, where it overhangs the anteromedial corner of the middle ear and may be separately distinguished as a tympanic process of the pterygoid. Inspection of these ridges indicates that they are ventrally abraded but not severely damaged, indicating also that the laminae were not produced into large, flaring plates. The pterygoid fossae delimited by the laminae are confined and shallow. In most of these respects, *Plesiorycteropus* sharply contrasts with armadillos, aardvarks, pangolins, and primitive ungulates, all of which have large, jutting medial pterygoid laminae (Patterson et al., 1992; cf. figs. 6, 8). There is some vague similarity to hyraxes, in which medial pterygoid lamina are poorly defined, but the resemblance is not marked.

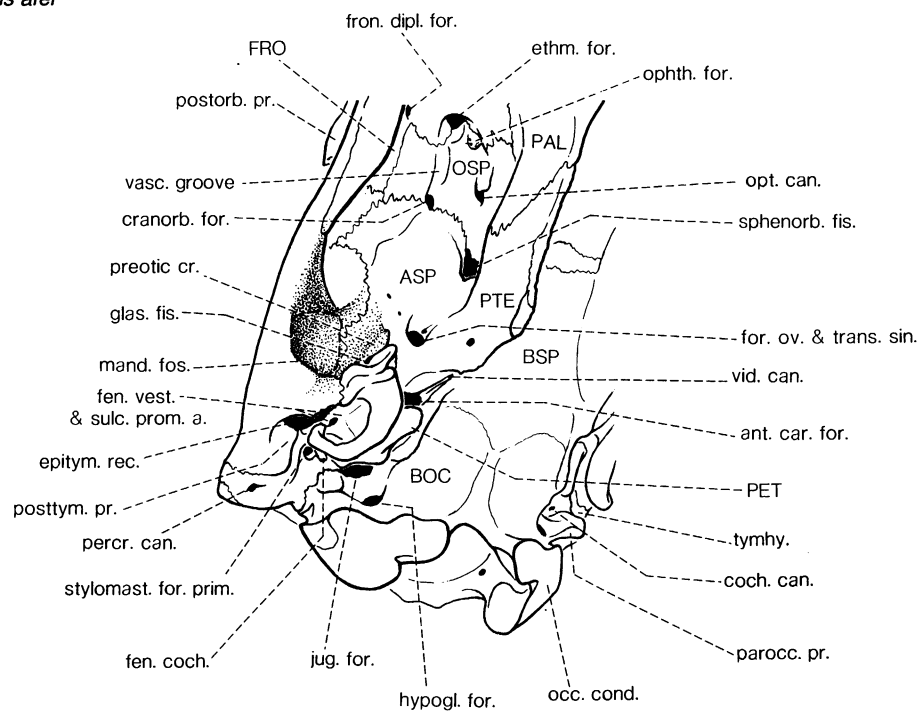
The inflated anterior portions of the sphenoid complex have no close parallel in the comparative set either. Armadillos and aardvarks inflate the sphenoid to a certain extent, but pneumatization principally affects endocranial surfaces, puffing out more dorsal

portions of the complex in the area behind the cribriform plate (figs. 6, 8). The closest morphological approach to the bibymalagasy condition that I am aware of is seen in extant talpids (e.g., *Talpa*), in which the lateral borders of the pterygopharyngeal region are similarly inflated by large airspaces (MacPhee et al., 1988, 1989). In hyraxes, the tuber maxillare extends a substantial distance posteriorly and presses up against the pterygoids (Fischer, 1986). However, this swelling never seems to actually invade pterygoid/sphenoid material. In bibymalagasy, there is no indication that what appear to be sphenoid sinuses are in fact situated within bone of maxillary derivation. Moreover, the swellings are so close together that—if interpreted to be tubera maxillares—no room is left between them for the choanae.

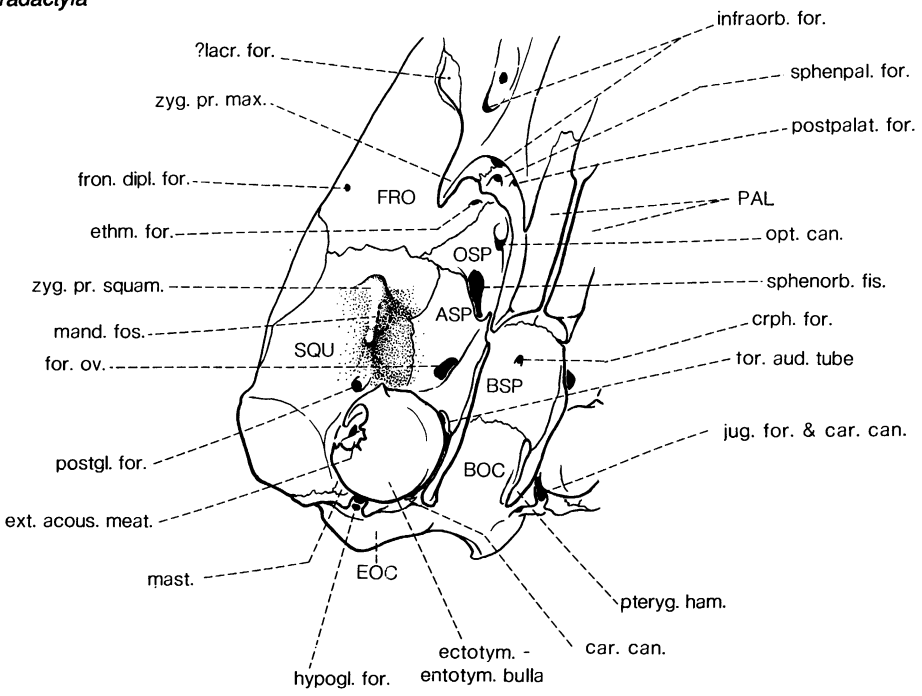
Another kind of structural boundary in this region also relates to pneumatization. As noted earlier, the sphenoid region is pneumatized by a paranasal sinus. Although the tympanic process of the pterygoid is replete with small vacuities (especially evident in MNHNP 328 and USNMP 474080; figs. 2C, 4D), these are not linked in any evident way with the pneumatic chambers in the sphenoid (as is the case in dasypodids, for example). It is more likely that these vacuities were formed by a pneumatic front emanating from the tympanic cavity, which would tend to support the identification of these pterygoid-derived eminences as tympanic processes (C 9). However, I note that because of breakage a definite pneumatic foramen linking these cellules and the middle ear cannot be confidently identified. There is no indication that the pterygoids were inflated by an extension of more dorsally situated paranasal sinuses, as occurs in extant sloths. The alternative possibility is that the pterygoid vacuities were filled with marrow rather than air; utilization of basicranial processes as sites for the formation of erythrocytes is believed to occur

→
Fig. 8. Oblique lateral view of orbital and infratemporal regions in representative members of comparative set (cf. fig. 6). All drawn to same rostrocaudal length; for relative sizes see figure 6. The region of the mandibular fossa is stippled in each specimen (cf. fig. 7). Limits of temporomandibular joints are enclosed by dashed ovals.

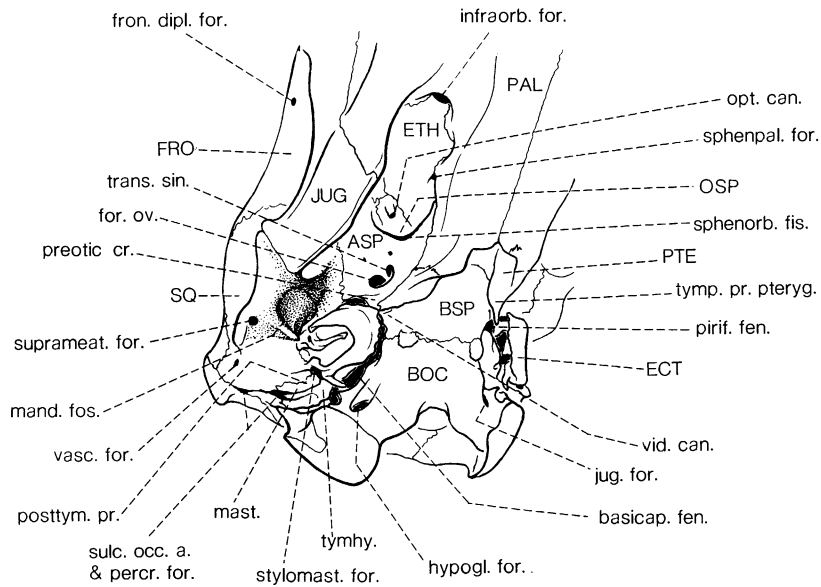
Orycteropus afer



Manis tetradactyla



Dasypus novemcinctus



Tamandua tetradactyla

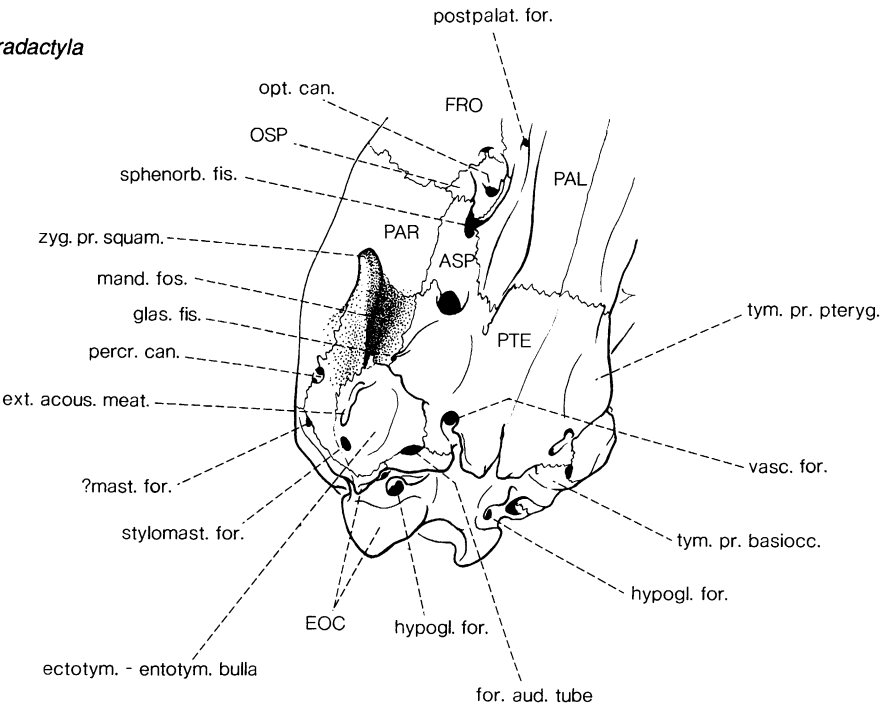
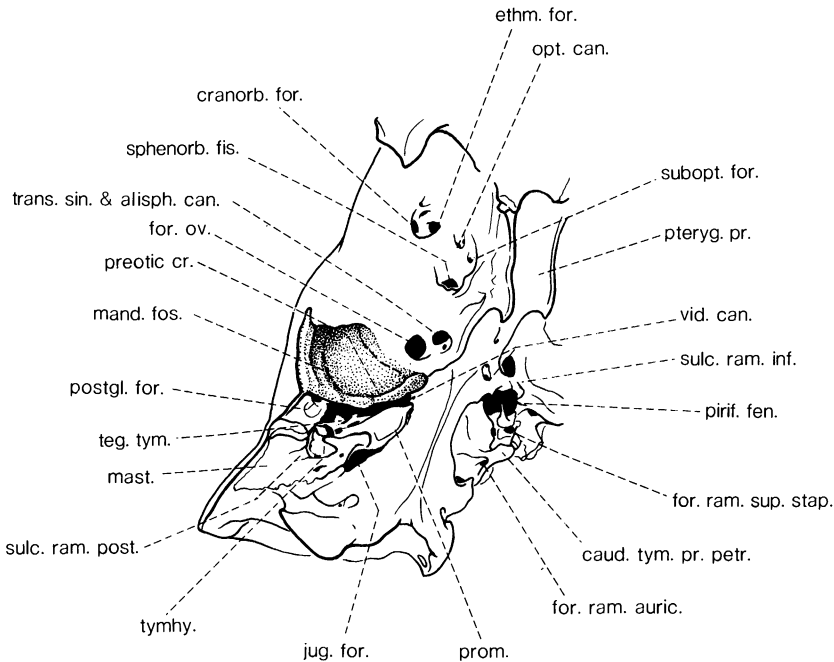


Fig. 8 (Continued)

Solenodon cubanus



Heterohyrax brucei

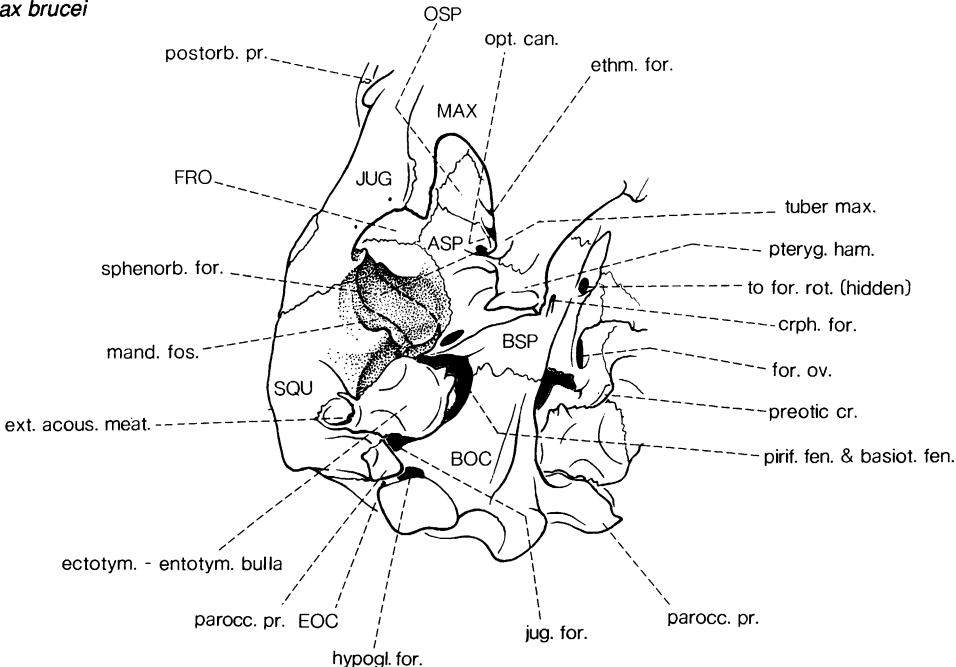


Fig. 8 (Continued)

in several extant lipotyphlans, although there is no reason at present to believe that this functional correlate is unique to these taxa (cf. MacPhee et al., 1988, 1989).

A complex series of channels passes through the substance of the pterygoids in the specimens with preserved basicrania, but it is very difficult to provide an unequivocal interpretation of these conduits. The largest one conforms to the usual position of the vidian (pterygoid) canal, and is so identified in the figures (e.g., fig. 5D). In addition to the nerves of the pterygoid canal, it may have transmitted emissary veins draining to the pharyngeal venous plexus, or possibly the "vidian artery," or perhaps all of these (cf. MacPhee, 1981).

Few features in the posterior part of the basicranial keel warrant special mention. The rear parts of the basisphenoid and the basioccipital are not obviously pneumatized and do not send out tympanic processes, but they bear noticeable ridges related to the attachment of longus capitis and other prevertebral muscles. The paroccipital process is small but distinct, and there is only one hypoglossal foramen on each side. As Filhol (1895) remarked, the occipital condyles are aardvark-like in the sense that they are somewhat kidney-shaped, with a marked waist in their midportions. However, condyles of similar design occur in lipotyphlans and many other land mammals, and are here regarded as morphologically primitive. The specialization seen in some armadillos (e.g., *Euphractus*), in which the anterior part of the condylar facet is separated from the main or posterior part, is not found in *Plesiorcyteropus*.

AUDITORY REGION

TYMPANIC FLOOR

Lamberton (1946: 30) concluded that *Plesiorcyteropus* lacked a bony bulla "as in *Orycteropus* . . . and *Manis*" (possibly a lapsus for *Dasypus*, since manids possess large bullae). This conclusion should be treated with caution because the extent to which ossified elements have been lost from the tympanic floor cannot be ascertained from existing material. On the other hand, the virtual absence of evident sutural surfaces in expected places

indicates that whatever bony elements were present were lightly affixed to the neurocranium.

None of the constant basicranial bones produced large tympanic processes in *Plesiorcyteropus*, the walls of the middle ear being instead defined by a series of very low ridges and projections (figs. 2C, 4D, 5D, 9). These are: anteriorly, the preotic crest and posterior margin of the medial pterygoid lamina (separately identified as the tympanic process of the pterygoid, C 9); medially, the rostral and caudal tympanic processes of the petrosal (both noticeably better developed in MNHNP 328 than in MNHNP 327; C 10); and laterally, the tympanohyal. The ectotympanic (not preserved) was probably but not certainly a narrow toroid, lightly connected to the skull, that did not form a large bulla. In favor of this interpretation is (1) absence of any part of the ectotympanic in the two skulls with partial or complete auditory regions, and (2) presence of a corrugated, suturelike surface on the tympanic wing of the squamosal, best interpreted as the contact site for the (unfused) anterior crus. Lamberton's (1946) and Thewissen's (1985) conclusions on these points are similar to mine, and need not be reviewed. Thewissen (1985) regarded the rostral and tympanic processes of the petrosal as being completely absent in MNHNP 327, but this is an overstatement (cf. fig. 5D). I prefer to interpret their small size as a species trait of *P. germainepetterae*. By contrast, *Orycteropus* lacks a caudal tympanic process of the petrosal, and probably also a rostral tympanic process, although this is hard to gauge because of the unusual, vertical orientation of its cochlear promontory (fig. 8). This orientation is not seen in *Plesiorcyteropus*. On the whole, tympanic floor constitution in *Plesiorcyteropus* is extremely primitive (cf. characterizations of eutherian basicranial morphotype by Van Der Klaauw, 1931; Novacek, 1977; MacPhee and Cartmill, 1986; MacPhee et al., 1988; C 10).

The preotic crest described earlier is more prominent in MNHNP 327 than in either MNHNP 328 or USNMP 474080, which I take to be a species difference. Preotic crests are present in *Orycteropus*, *Dasypus*, numerous lipotyphlans, and many other mammals

(McDowell, 1958; MacPhee, 1981; fig. 8). When present the crest usually acts as a support for the anterior leg of the ectotympanic, or helps to form one wall of the glaserian fissure. Patterson (1975: 231) regarded the aardvark version of this outgrowth as the homolog of a similarly positioned crest (his "styloid process") found in *Meniscotherium*, *Phenacodus* and *Hyopsodus* (Gazin, 1965), but he did not explicitly mention that it occurs in *Plesiorhycteropus*. In *Orycteropus* the crest buttresses the ectotympanic, but does not contact the mandibular condyle (fig. 8); it presumably had a similar function in these extinct primitive ungulates. By contrast, modification of the crest into a "pseudoglenoid process" to act as a mandibular backstop is very rare.

It should be noted that it is not inconceivable that a small, pyramidal entotympanic filled the gap between the ectotympanic and the ventral surface of the promontorium. One reason for so thinking is that the whole apical end of the promontory is denticulated and roughened, as though it articulated with a bone now missing (fig. 2C). (Thewissen [1985: 274, fig. 4] interpreted this roughened area as a lingula shielding the hiatus of the facial canal.) Similar conditions are found in *Tolypeutes*, in which a small entotympanic is interposed between the promontorium and the ectotympanic. In *Orycteropus* the entotympanic is said to be completely absent (Van Der Klaauw, 1931). Condylarthrans are assumed to have had the ectotympanic alone in their tympanic floors (cf. Cifelli, 1982; Prothero et al., 1988; for some positive evidence of this in *Ectocion*, see Thewissen, 1990).

TYMPANIC ROOF

In *Plesiorhycteropus* the tympanic roof is largely formed by the petrosal (fig. 9), with smaller contributions by the sphenoid (alisphenoid) and squamosal—an uncommon pattern (MacPhee, 1981; C 11). The squamosal makes a large contribution in aardvarks and pholidotans, and in both of these groups this bone is deeply inflated by epitympanic sinuses. I agree with Thewissen (1985) that no epitympanic sinus occurs in *Plesio-*

rycteropus, but I disagree with his identification of a petrosal pneumatic foramen (see Pneumatization). Because both MNHNP 327 and 328 have been broken and repaired on several occasions, it was difficult to tell whether any of the gaps in the tympanic rooves of these specimens represented a true piriform fenestra ("foramen lacerum medium" of Patterson [1975]) or merely inept patching jobs. The new Anjohibe skull (fig. 4D) proves that the piriform fenestra was present but small in bibymalagasy, which may be regarded as another primitive eutherian feature. In bibymalagasy there is also a distinct gap between the cochlear surface and the central stem (basiotic fissure), continuous with the jugular foramen, but this feature is seen in many mammalian groups and I regard it as a primitive trait (MacPhee, 1981).

In the absence of any evidence concerning petrosal ontogeny in *Plesiorhycteropus*, I will assume that the entire contribution of this bone to the tympanic roof is represented by the tegmen tympani. This is not unreasonable in any case, because there is no indication of a separately formed petrosal epitympanic wing (cf. MacPhee, 1981). The tegmen runs in an unbroken sheet from the canalicular portion of the petrosal to the transverse level of the promontory's anterior pole. Tegmina of equivalent size are not frequently found in living mammals, suggesting that large ones are derived (MacPhee, 1981; MacPhee and Cartmill, 1986; C 11).

Although a large tegmen tympani may be cited as one of the few, definitely derived cranial traits of bibymalagasy, except for the position of the foramen for the ramus superior (C 16) other features of the tegmen are basically primitive. The facial nerve traveled in an unenclosed sulcus after leaving foramen faciale; the epitympanic recess and the related fossa incudis are of insignificant size; and the mastoid cavity is absent. There is a fossa for the tensor tympani, but I find that it is restricted to the tegmen tympani and does not clearly lap onto the sphenoid epitympanic wing, which is the reverse of Thewissen's (1985) interpretation. By contrast, the stapedial fossa is fully (and therefore primitively) exposed on the sidewall of the auditory capsule, where it is separated from the ter-

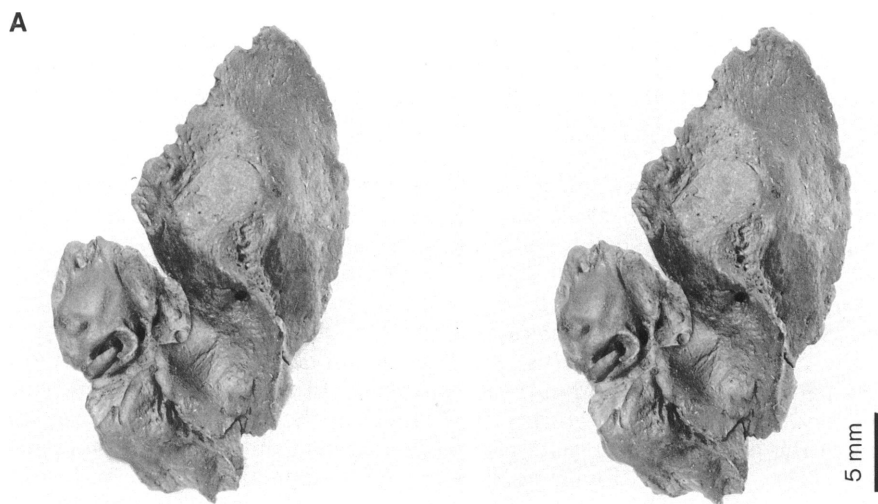
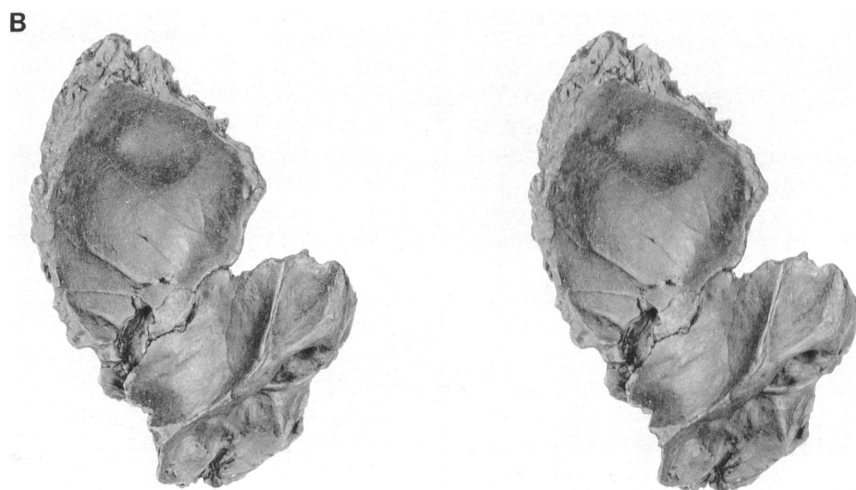


Fig. 9. Left auditory region of *Plesiorycteropus madagascariensis* MNHNP 328 (Belo skull), before reassembly. Stereopair views (with keys): **A**, ectocranial surface (asterisk indicates apparent border of mandibular fossa as defined by attachments of craniomandibular joint capsule); **B**, endocranial surface (double asterisks indicate approximate position of exit foramen for stapedial ramus superior on ectocranial side).



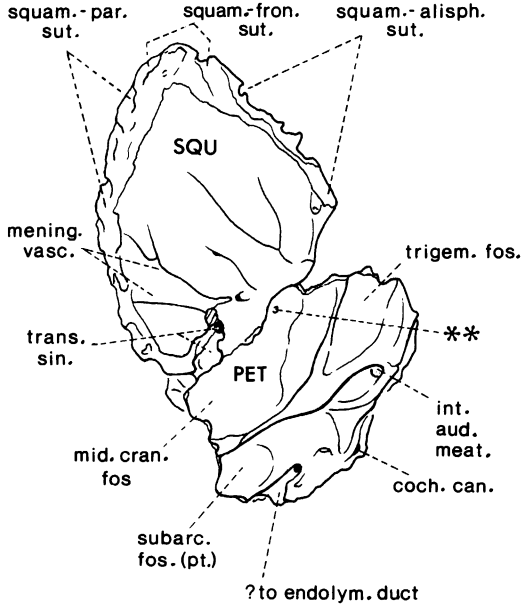
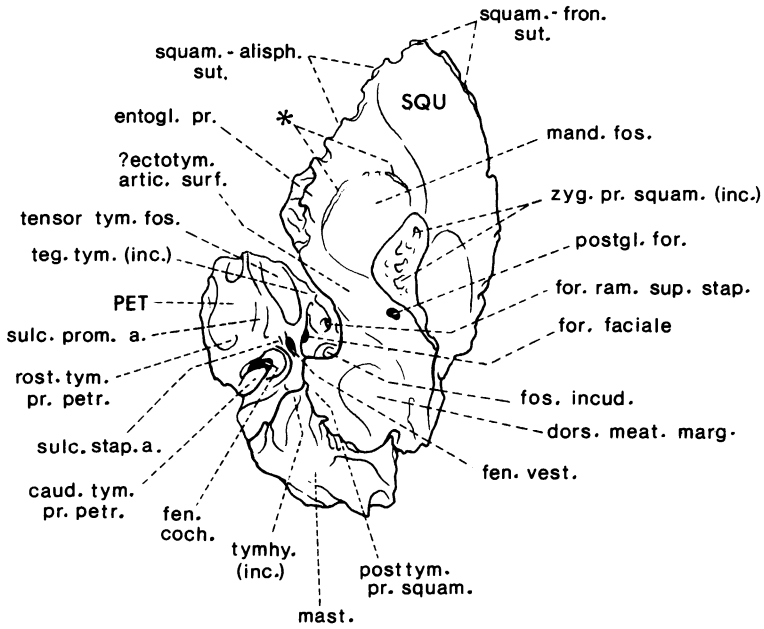


Fig. 9 (continued)

minial part of the facial sulcus ("foramen" stylomastoideum primitivum) by a slight ridge. The tegmen is not internally inflated and thus differs from the condition reported for condylarthrans (Cifelli, 1982).

Processus cristae facialis, regarded by Patterson et al. (1989: 7) as "characteristic of the Xenarthra as a whole," is not present in *Plesiorhycteropus*. There are ridges on the tegmen tympani that are in the position of this process in some armadillos (especially *Prionodontes*), but they do not form the large, multilamellar structure seen in dasypodids.

The small epitympanic wing of the sphenoid is steeply inclined (fig. 5D). In MNHNP 327 there is a pronounced groove on the sphenoid tympanic wing that seems to connect with another groove leading from the aperture interpreted as the foramen for the ramus superior of the stapedia artery. This groove may have held the ramus inferior (and possibly the lesser petrosal nerve as well). Similarly positioned grooves are found on the other two skulls with intact basicrania. There is no alisphenoid canal, but there is a prominent groove on the alisphenoid that probably carried the ramus inferior after it left the tympanic cavity (best defined in USNMP 474080). The squamosal epitympanic wing contributes an articular area for the anterior crus of the ectotympanic, but it dwindles to a small shelf caudally.

A well-developed posttympanic process that presses against but does not completely enwrap the large tympanohyal (fig. 7) is a salient (albeit primitive) feature of the bi-bymalagasy auditory region. The posttympanic process defines the posterior margin of the external acoustic meatus, which is dorsally shielded by a continuation of the line of the zygomatic process of the squamosal. Although quite large in all specimens, the tympanohyal seemingly did not contact the promontorium. There is no sign, in the form of broken margins or sutural contacts on the roof, that the ectotympanic was elongated into a tube. A small postglenoid foramen is situated on the sloping posterior aspect of the zygomatic process of the squamosal. In all of these features, *Plesiorhycteropus* resembles some dasypodids (e.g., *Dasypus*) as much as aardvarks (fig. 6); very similar meatal areas are also seen in many lipotyphlans (and other

eutherians). By contrast, hyraxes differ in having a greatly expanded squamosal that covers all of the mastoid region, and they lack the postglenoid foramen (fig. 6).

Most of the salient features of the promontory have already been referenced. The promontory itself is somewhat teardrop-shaped (fig. 9A). On its medial side is a comparatively small but broadly exposed cochlear canaliculus, morphologically separated from the fenestra cochleae by a wide process recessus (figs. 2C, 5D). Thewissen (1985: 275) stated that the aperture of the cochlear canaliculus opens dorsally in *Plesiorhycteropus* but more ventrally in *Orycteropus*. I find that there is practically no difference between these two taxa in this regard, and I regard the position of the canaliculus as "ventral" in both (cf. figs. 5D, 8). In advance of the canaliculus is a narrow shelf that encloses a groove for the inferior petrosal sinus. Radiographs reveal that the cochlear duct was spiraled and completed about two and one-half turns.

MASTOID REGION

The mastoid portion of the petrosal bone is primitively well exposed in lateral and occipital view (fig. 2B, D), a feature also seen in aardvarks and lipotyphlans but strikingly different from conditions in hyracoids, manids, and most xenarthrans (fig. 6; C 12).

Several foramina typically penetrate what is loosely termed the mastoid region in comparative anatomy. The two that are of greatest interest in this analysis are the mastoid foramen and the percranial canal, the separate identities of which have often been misunderstood in the past (for a morphological differentiation of these terms, see C 13). Here it will suffice to note that *Plesiorhycteropus* lacked a mastoid foramen but possessed a percranial canal, whereas *Orycteropus* seemingly possesses both. The percranial canal carries the great diploetic artery (arteria diploetica magna; Wible, 1987), which in *Plesiorhycteropus* presumably arose from the occipital artery near the triple junction of the mastoid, parietal, and occipital. Because of damage to this region, the existence of this foramen is obvious only in USNMP 474080 (fig. 4B, C), although in the other skulls the vascular groove (?for the occipital artery) can

easily be identified. There are a number of tiny foramina on the occipital aspect of the bibymalagasy skull (figs. 2B, 4B), but these exhibit no consistent positioning or symmetry in the available material and none is therefore counted as the equivalent of the large, constant mastoid foramen of *Orycteropus* (fig. 6).

PNEUMATIZATION

Middle-ear pneumatization in *Plesiorycteropus* is trivial. Especially noteworthy is the absence of the enlarged epitympanic sinus found in *Orcyteropus* (Le Gros Clark and Sonntag, 1926; C 14). Thewissen (1985) identified, as a "pneumatic foramen," a channel that he found in the rear of the tympanic cavity in the then-detached right petrosal of MNHNP 328. In identifying this structure he may have been influenced by Cifelli's (1982) recognition of a possible pneumatic foramen ("posterior petrosal epitympanic sinus") in *Phenacodus* and *Meniscotherium*. Close study of the right petrosal of MNHNP 328 convinces me that Thewissen's channel is vascular: it opens into the transverse sinus, not into the bone of the mastoid region. However, I do not know what the homolog of the vessel in question may be. It is too posterior in position to be a track for the ramus superior, and there is a better candidate for a groove for the ramus posterior (see Vascular Features).

The posteroexternal surface of the mastoid is damaged in MNHNP 328, allowing inspection of bone texture. While it is true that the bone in this part of the mastoid is weakly honeycombed, I could not find any linkage between the small vacuities therein and any part of the tympanic cavity. In any case, significant mastoid pneumatization is certainly absent.

VASCULAR FEATURES

As Thewissen (1985) noted, there is a well-defined groove on the ventral surface of the cochlear housing in *Plesiorycteropus* that can only be interpreted as a sulcus for the promontorial artery (fig. 7). The groove begins posteromedially, immediately in front of the ventral lip of the aperture of the fenestra cochleae, then swings in a wide arc to ter-

minate on the anterior pole of the promontory. This is the transpromontorial routing of the promontorial artery (C 17), usually considered to be primitive for eutherians (Cartmill et al., 1981; MacPhee and Cartmill, 1986; Wible, 1987; but see Rougier et al., 1992; Novacek, 1993b).

The anterior carotid foramen is not preserved in MNHNP 327 and 328 because of breakage, and both Lamberton and Patterson seemed to have been unsure of its position. Patterson's (1975: 211, fig. 15) "f. car.?" is unquestionably the rostral portion of the basiotic fenestra; the true anterior carotid foramen, not well preserved in this specimen, is located in the sphenoid wing in USNMP 474080, separate from and medial to the position of the piriform fenestra (Patterson's "foramen lacerum medium"). On the basis of endocast morphology, Thewissen (1985) concluded that, in relative terms, the promontorial artery (or its endocranial continuation, the cerebral carotid artery) of bibymalagasy was much smaller than that of *Orycteropus*.

The only branch that the promontorial artery normally releases within the confines of the tympanic cavity is the stapedia. Thewissen (1985), not finding a sulcus for the stapedia artery on the petrosal nor a foramen of exit for the stapedia ramus superior in the tympanic roof, inferred that the stapedia artery was probably absent in *Plesiorycteropus*. I find that both of these features are uniformly present in the three specimens preserving the basicranium (figs. 2C, 4D, 5D). The sulcus for the (proximal) stapedia artery departs from the larger and better-defined sulcus for the promontorial artery immediately ventral to the lip of the fenestra vestibuli. This channel then crosscuts the sulcus for the facial nerve, and, proceeding laterally, terminates at a foramen in the anterolateral part of the tegmen tympani. This foramen is quite distinct from foramen faciale, the intratympanic opening for cranial nerve VII. The foramen for the ramus superior is illustrated in Patterson's drawing reproduced here as figure 10C ["f.st?"]. The promontorial artery and stapedia ramus superior were of about even caliber, judging from the widths of their foramina of exit.

Primitively, the proximal stapedia splits

into superior and inferior rami on the tympanic roof. It seems to be an inviolate rule that the ramus superior, when present, must pass through the obturator foramen of the stapes on its way to the endocranium, where it ramifies into meningeal supply vessels (see Novacek and Wyss, 1986). The ramus inferior proceeds anteriorly, leaving the middle-ear cavity through the glaserian fissure or sometimes through a separate foramen in the bulla or the preotic crest (MacPhee, 1981). As noted previously, the stapedia ramus inferior seems to have been present in *Plesiorhycteropus*, because portions of a groove can be followed from the foramen for the ramus superior to a position just medial to the preotic crest (figs. 4D, 5D). The stapedia system of *Plesiorhycteropus* may have possessed a third branch, the ramus posterior. At present the sole basis for this inference is a deep groove seen on the rear surface of the caudal tympanic process of the petrosal. There is not, however, a definite channel connecting this groove with the one for the proximal stapedia. It is just as plausible, and possibly more so, to infer that the groove is actually for a nerve (?auricular ramus of vagus). *Solenodon* possesses large grooves and apertures for each of these structures (fig. 8).

Putting aside the question of the existence of the ramus posterior, *Plesiorhycteropus* must be regarded as simply primitive in having an otherwise unreduced carotid system in the middle-ear region. Equally plesiomorphous is the absence of any evidence of bony canals surrounding portions of the network within the middle-ear cavity. In these respects *Plesiorhycteropus* resembles the majority of lipotyphlans, generally thought to exhibit among extant eutherians the most primitive pattern of arterial circulation within the middle ear. Aardvarks have retained most of the primitive pattern but have lost the ramus inferior (Thewissen, 1985). Xenarthrans, however, have lost the latter vessel as well as the proximal stapedia, a common derived pattern (Wible, 1987). It is generally accepted that condylarthrans possessed both a stapedia and a promontorial sulcus (Cifelli, 1982; Prothero et al., 1988), with the ambiguous exception of *Hyopsodus* which lacks the stapedia sulcus. Thewissen (1990), however, has challenged Cifelli's identification of a stapedia sulcus in *Phenacodus intermedius*.

Grooving the anteriormost margin of the basiotic fenestra, immediately medial to the tympanic process of the pterygoid, is a feature which could be interpreted either as the sidewall of a vascular hemicanal or as a crest associated with the attachment of prevertebral musculature (figs. 4D, 5D). If the structure is related to the passage of a vessel, the inferior petrosal sinus is the likeliest possibility (MacPhee, 1981). (The internal carotid's pathway as described above seems to me beyond doubt, and I question whether a hypertrophied ascending pharyngeal artery would have left an impression of this sort.) In MNHNP 327 the feature is less channel-like and is perhaps better interpreted as the lateral margin of the attachment area of longus capitis.

ENDOCRANIAL SURFACE OF PETROSAL

In bibymalagasy the subarcuate fossa is negligible (Thewissen, 1985; C 15), but the posterior part of the trigeminal fossa is exceptionally well defined (fig. 9B). These fossae are bordered by a sharp petrosal crest. Although the crest continues onto the internal sidewall of the skull, as it does in many mammals, it is certainly not developed into the exaggerated tentorial lamella seen in manids and carnivores. The petrosquamous sinus is almost entirely enclosed by a canal, from which emanate small tracks for meningeal vessels.

CRANIAL ROOF AND OCCIPITAL REGION

CRANIAL ROOF

In lateral view, the outline of the cranial roof bulges over the cerebral hemispheres, then dips and flattens on the rostrum (figs. 2D, 3B, 4C, 5C). In dorsal view, cerebral bulging is more accentuated in *Plesiorhycteropus germainepetterae* than in *P. madagascariensis*, and in the former the orbital constriction is more pronounced. The squamae are not dorsally extensive and the zygomatic process is not laterally projecting, with the result that very little of the squamosal can be seen in dorsal perspective. This is a similarity to manids as well as xenarthrans, most of which have small squamosal squamae.

The sutures in the preorbital region of the

skull, to the extent that they are known, have already been described. The parietals are large compared to the frontals, a point of similarity to armadillos (and to a lesser extent, hyraxes) not shared by armadillos, myrmecophagids, and pholidotans, in which the frontals are much elongated (figs. 2A, 4A, 6). The lambdoid suture runs just anterior to the nuchal crest, so that a narrow band of the supraoccipital is exposed in dorsal aspect, as in many members of the comparative set (figs. 2A, 6). Uniquely in USNMP 474080, sutures are still completely patent and an interparietal is clearly present (fig. 4A). Tubulidentates are said to lack the interparietal, and this feature is sometimes used as part of the diagnosis of the group (e.g., Shoshani et al., 1988). However, I confirm Parker's (1885) observation that the interparietal is distinctly present in very young armadillos (e.g., AMNHM 51395). In dorsal view the outline of the nuchal crest is broadly interrupted in its middle portion in *P. germainepetterae*, as in most dasypodids, hyraxes, and *Meniscotherium* (fig. 6; see also Gazin, 1965). The large "bosses" on the nuchal crest of most armadillos (fig. 6) are absent.

A number of small foramina perforate the summit of the neurocranium in *Plesiorycteropus* (figs. 2A, 3A, 4A, 5A). This is also true of *Orycteropus*, *Meniscotherium*, *Phenacodus*, and larger dasypodids and manids (fig. 6). In addition to these small apertures there is a variable number of larger ones, situated low on the parietal. In the Ambolisatra calvarium it was possible to determine that they open into meningeal grooves endocranially (fig. 3C). Variably among eutherians (cf. fig. 6), foramina in similar positions with similar relations conduct meningeal divisions of the ramus superior (rami temporales), although in other cases they seem to be venous ports only (MacPhee and Cartmill, 1986; MacPhee, 1987; "squamosal sinus-canal" of Novacek, 1986).

The only other notable features on the roof are the temporal lines, which are situated approximately midway on the cranial sidewalls and are rather similar in disposition to the equivalent lines in *Orycteropus* (figs. 2A, 5A, 6). They converge posteriorly, but do not meet in the midsagittal area (cf. also hyraxes). The lines are better developed and more closely approximated in MNHNP 328 and USNMP

474080 than in MNHNP 327, even though the former specimens are evidently immature. Temporalis markings are virtually absent in myrmecophagids, pholidotans, and most small armadillos, but tend to be strong in all other members of the comparative set (fig. 6). In hairy and scaly anteaters, the absence of strong markings probably reflects an absolutely small temporalis mass.

OCCIPITAL REGION

Among the very few justifications that Filhol (1895) provided for regarding *Plesiorycteropus* as a relative of *Orycteropus* was similarity in the shape of the occipital (figs. 2B, 4B, 6). In both taxa the occipital planum is essentially vertical and flat, a point of major contrast to myrmecophagids and pholidotans but not to lipotyphlans, armadillos, hyraxes, and a host of other mammals. As previously noted, mastoid exposure is relatively pronounced in occipital view in bibymalagasy, another primitive feature (C 12). In definite contrast to armadillos (fig. 6), the margin of the supraoccipital that forms the dorsal rim of the foramen magnum is not notched in *Plesiorycteropus*. Large true condyloid canals (sensu McDowell, 1958) are to be found on the posterior aspect of the occipital, just above the position of the occipital condyles (fig. 2B). These canals, which are absent in *Orycteropus*, join the sigmoid sinuses and are similar to canals transmitting the ultimate cranial extensions of the longitudinal vertebral sinuses in *Canis* (Reinhard et al., 1962). They are also seen in many lipotyphlans (*Solenodon*, chrysochlorids, potamogalines; McDowell, 1958). The position of the true mastoid foramina is discussed above (see Mastoid Region).

The occipital condyles of bibymalagasy are well separated, as they are in most members of the comparative set (fig. 6). (Curiously, Gregory [1910: 335] incorrectly claimed that the condyles were continuous across the basioccipital in *Orycteropus*.)

ENDOCAST AND ENDOCRANIUM

Thewissen (1985) made latex endocranial casts of MNHNP 327 and 328, denoted here as MNHNP 327E and 328E. Different latex media were evidently utilized in making the two endocasts, because they differ in color

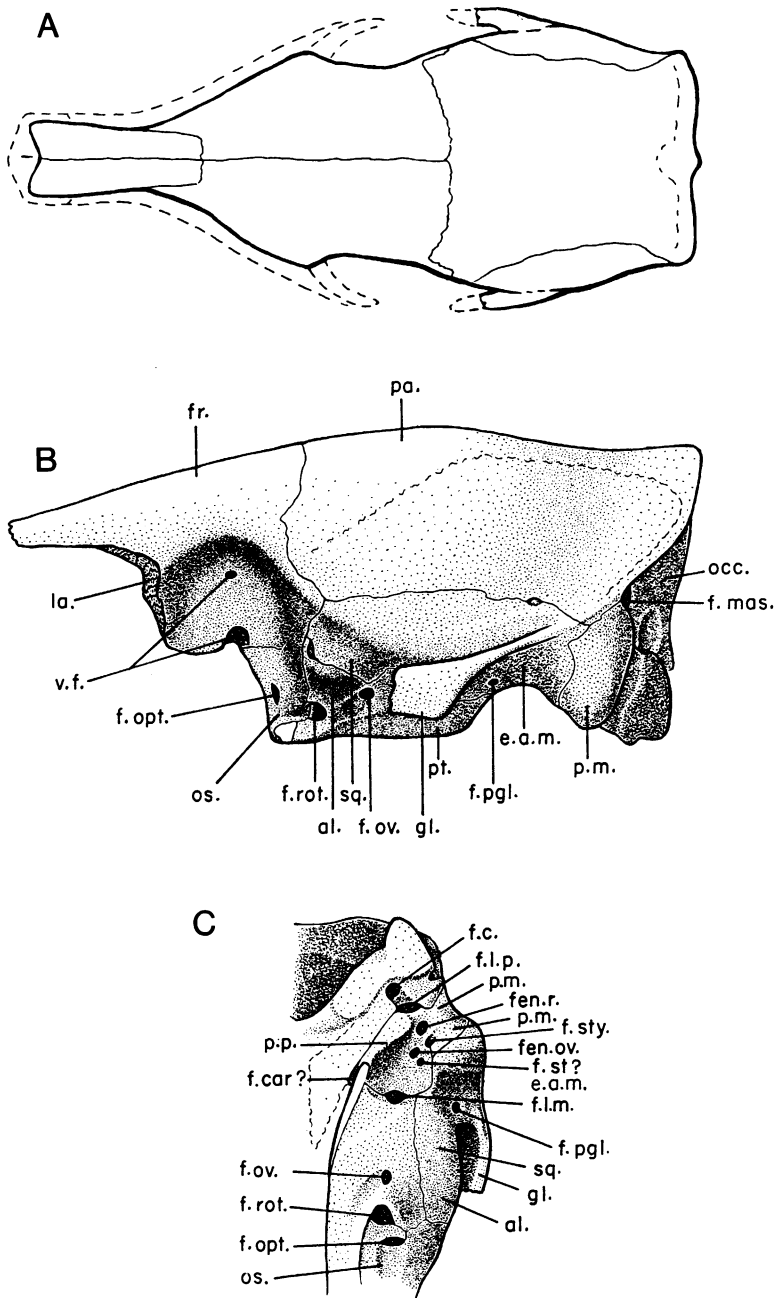


Fig. 10. Patterson's (1975: figs. 14 and 15) schematic depictions of (A) dorsal, (B) left lateral, and (C) right basicranial views of skull of *Plesiorycteropus*, mostly based on MNHNP 327. Errors in identification are noted in the following emended key: **al.**, alisphenoid (in C leader terminates on squamosal, not alisphenoid); **e.a.m.**, external auditory meatus (leader omitted); **f.c.**, condylar (hypoglossal) foramen; **f. car?**, part of basiotic fenestra (and not "[anterior] carotid foramen"); **f.l.m.**, piriform fenestra or artifact ("foramen lacerum medium"); **f.l.p.**, jugular foramen (= foramen lacerum posterius); **f. opt.**, optic canal; **f. ov.**, foramen ovale; **f. pgl.**, postglenoid foramen; **f. rot.**, foramen rotundum (separate spheno-orbital foramen, not indicated by Patterson, may be misidentified as "f. opt." in C); **f. sty.**, foramen stylomastoideum primitivum (but leader points to fenestra vestibuli); **fen. ov.**, fenestra ovalis (but leader points

TABLE 8
Plesiorycteropus: Endocast "Size" Modules

Endocasts	Measurements ^a				Module A		Module B	
	1	2	3	4	1 × 3 × 4	Ratio (B/A)	2 × 3 × 4	Ratio (B/A)
A. MNHNP 328E	43.4	33.3	33.6	15.4	22456.9	74.2	17230.8	72.9
B. MNHNP 327E	37.8	28.5	31.7	13.9	16655.8		12558.0	

^a Measurements (in mm) are: 1, Length, middle of sulcus between olfactory lobe and neopallium to posteriormost point on vermis, measured in midsagittal plane. 2, Length, middle of sulcus between olfactory lobe and neopallium to a line passing through middle of sulcus between neopallium and vermis, measured in midsagittal plane. 3, Width, biparietal. 4, Height, middle of dorsal rim of foramen magnum to dorsalmost point on vermis, in midsagittal plane.

and resiliency. The few measurements that could be compared between endocasts and crania indicate that the shrinkage factor is negligible. MNHNP 328E was complete enough to permit estimation of brain size in *Plesiorycteropus germainepetterae* (table 14).

Except for their substantial difference in size, the two endocasts agree in most observable details. Due to the incompleteness of the ventral sides of the skulls, detail is poor on the undersides of the endocasts, particularly in the rostral portion. From the dorsal side, the usual divisions between the olfactory lobes, cerebral hemispheres, and hindbrain are clearly demarcated. Outstanding features are: (1) absence of any flexure, (2) neopallium not extended over olfactory lobes, and (3) neopallium comparatively small, as judged by the relatively dorsal position of the rhinal sulcus.

Thewissen's (1985) well-documented report on the endocasts indicates that both *Plesiorycteropus* and *Orycteropus* are pervasively primitive, with neither displaying strong resemblances to ungulates in his estimation. Equally interesting is the finding that bibymalagasy are also quite different from aardvarks in endocast morphology, which Thewissen (1985) noted in his structure-by-structure comparisons but did not comment

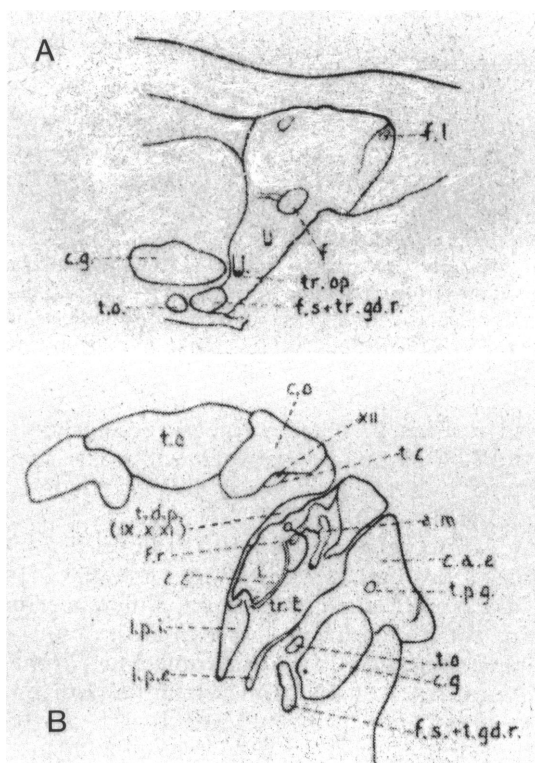
on in his conclusions. Thewissen (1985) emphasized that the olfactory lobes of *Plesiorycteropus* are less extensive than those of *Orycteropus*. This appears to be true in terms of their rostral extent, but laterally they seem to have been extensive and rather compressed, in the manner of the "short" lobes described for *Manis* (cf. Weber, 1891; Elliot Smith, 1899; Friant, 1960; Hackethal, 1976).

Bibymalagasy and aardvarks are characterized by extremely well-defined, essentially horizontal rhinal sulci that divide the neopallium from the piriform lobe. However, the sulcus of *Plesiorycteropus* occupies a higher position on the cerebral surface than it does in *Orycteropus* (cf. Elliot Smith, 1899), with the result that it is visible from the dorsal aspect. The piriform lobe is large but does not project laterally to the very noticeable degree seen in *Orycteropus* (Gervais, 1869; Friant, 1960).

The large, roughly triangular area located between the posterior aspect of the neopallium and the vermis is flat and featureless in both bibymalagasy endocasts. This is a common finding in mammalian endocasts and neither proves nor disproves the presence of midbrain exposure (Jerison, 1973). For example, although midbrain exposure certainly occurs in *Solenodon*, this fact cannot be re-

←
to foramen faciale); **fen. r.**, fenestra rotunda (cochleae); **fr.**, frontal; **gl.**, glenoid process (= zygomatic process of squamosal); **la.**, frontolacrimal suture; **occ.**, occipital; **os.**, orbitosphenoid; **pa.**, parietal; **p.m.**, pars mastoidea; **p.p.**, pars petrosa; **pt.**, pterygoid; **sq.**, squamosal; **v.f.**, vascular foramina (= frontal diploic and ethmoid foramina). Abbreviations **f. st?** and **f. mas.**, not listed in original key, identify exit foramen for stapedia ramus superior and the percranial canal, respectively.

Fig. 11. Schematic depictions of (A) orbital and (B) otic regions of skull of *Plesiorhycteropus*, from Lamberton's (1946: pl. IV, figs. 16 and 17) monograph. Identity of illustrated specimen not mentioned, but is probably MNHNP 327 (cf. fig. 5C). Original illustrations were unaccompanied by keys to abbreviations; however, Lamberton's intended identifications can be inferred in most cases: **a.m.**, mastoid process (= tympanohyal); **c.a.e.**, external acoustic meatus (dorsal border); **c.c.**, ?groove for promontorial artery; **c.g.**, mandibular fossa (as understood by Lamberton; in this paper, region indicated also includes fossa for lateral pterygoid muscle); **c.o.**, occipital condyle; **f.**, foramen (= ethmoid foramen); **f.l.**, lacrimal foramen; **f.r.**, fenestra cochleae; **f.s. + tr. gd. r.**, "spheno-orbital fissure + foramen rotundum" (but in reality = foramen rotundum only); **l.p.e.**, lateral pterygoid lamina; **l.p.i.**, medial pterygoid lamina; **t.c. XII**, hypoglossal foramen; **t.d.p. IX, X, XI**, posterior lacerate foramen; **t.o.**, foramen ovale (also designates foramen magnum); **t.p.g.**, postglenoid foramen; **tr. op.**, "optic canal" (but in reality = spheno-orbital foramen; unlabeled foramen anterodorsal to "tr. op." is true optic canal); **tr. t.**, ? (possibly refers to groove for auditory tube, or roof of tympanic cavity).



trieved from endocast impressions because the endocranial roof does not mimic the shape of the corpora quadrigemina (Bauchot and Stephan, 1967).

The most obvious gross difference between the endocasts is that MNHNP 328E is considerably larger than MNHNP 327E, which I regard as strong evidence for assigning these skulls to different species (see Material, Taxonomy, and Occurrence). Because most of the right sidewall of the neurocranium is missing in MNHNP 328E, its endocranial volume cannot be accurately computed. I therefore devised two endocranial "volume" modules (table 8) as a means of comparing them. As a measure of actual endocranial volume, these modules are hopelessly inadequate. However, considered merely as estimates of free volumes enclosed by homologous landmarks, they provide some basis for inferring the scale of size differences.

Because the size of the olfactory lobes is not adequately reflected in the endocasts, two different measurements of length were used (neopallium + vermis length for module A, neopallium length only for B). The ratios of

the measurements used for these modules are very similar; both show that the module of endocranial "volume" for MNHNP 327 is only 73–74% of that for MNHNP 328. This is a considerable difference, matched (within species) only by differences observed in markedly sexually dimorphic primates (e.g., *Gorilla gorilla*; data of Holloway, 1980). Whether the contrast between these two individuals is representative of the populations from which they came will have to be settled with additional material (see below). Yablokov (1974) shows that the coefficients of variation for absolute brain weight within populations of small mammals are on the order of 6–7%, while they are about twice that (12–15%) for adult body weights. I have no intrasexual brain weight data for *Orycteropus*, although *O. afer* is said not to be significantly dimorphic in body size (Shoshani et al., 1988).

There are no endocasts for MNHNP 534 or USNMP 474080. However, the endocast of MNHNP 328 fits comfortably inside the Ambolisatra skull, indicating that its cranial cavity was at least as large as (if not larger than) that of the Belo specimen.

MORPHOLOGY OF THE POSTCRANIUM

VERTEBRAL COLUMN

A total of 34 vertebrae (including sacral elements) attributable to *Plesiorhycteropus* have been identified in museum collections. The total sample probably includes vertebrae of both species, but with the exception of the Ambolisatra specimens (which, if the skull-vertebrae association is valid, belong to *P. madagascariensis*), no effort has been made to sort them taxonomically. I assume that bibymalagasy possessed the primitive number of cervical vertebrae (seven), although the atlas (fig. 12) is the only cervical element identified to date. There is evidence for seven sacrals and as many as five or six lumbar, but the number of thoracics and caudals is quite uncertain. The very gradual diminution in size of the associated anterior caudals from Ambolisatra (fig. 20) implies that the tail was long. Of the 16 presacrals in the available collections, only two (both lumbar vertebrae; figs. 14, 17) preserve intact spinous processes (neurapophyses). In both cases the spinous processes are long and narrow, and were probably subvertical in orientation in the living animal. Rostrad, the stumps preserved on some anterior thoracics indicate that anterior neurapophyses were more recumbent. Hypapophyses for caudal vasculature have not been found, but the small bumps on the venters of many vertebral centra may be articular platforms for these structures.

Lamberton (1946) believed that the spinal column of *Plesiorhycteropus* was too poorly sampled for him to be certain that xenarthrous articulations were absent. But there is certainly no hint of xenarthry or multielement synostoses (other than those involving sacral elements) in the axial skeleton as currently known, and I agree with Patterson (1975) that *Plesiorhycteropus* lacked supernumerary articulations (C 18).

CERVICAL VERTEBRAE

Two cervical vertebrae were found in marked boxes containing *Plesiorhycteropus* remains in the MNHNA collection: an atlas, broken in two halves with parts missing, and a ?lower cervical, largely intact. Only the atlas is referenced by Lamberton (1946) and Patterson (1975).

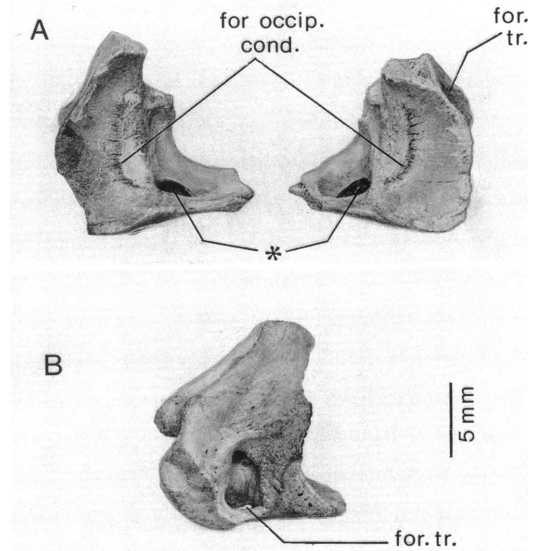


Fig. 12. Atlas, *Plesiorhycteropus* sp. MNHNA 1987.043A. A, anterior (craniad), and B, left lateral views. Asterisk, intervertebral foramen (for first cervical nerve and vertebral artery) piercing dorsal aspect of neural arch.

The atlas is basically primitive in form and has few distinctive features (fig. 12). The vertebral artery followed a tortuous course through the lateral mass and neural arch, to emerge through an aperture (first cervical intervertebral foramen) that primitively transmits the first cervical spinal nerve. This aperture additionally conducted a vessel (probably a vein) to or from a small canal situated medial to the foramen transversarium. This small canal is absent in the atlases of Malagasy lemuriforms, viverrids, and muroids, which helps to confirm its distinctiveness. This canal is also absent in *Orycteropus* and *Manis*, although there are tiny foramina in the same region that may have carried branches of a homologous vessel.

MNHNA 1987.043B (not illustrated here) is a middle or lower cervical that was included with the *Plesiorhycteropus* bones from Ampoza. There are enough general correspondences between this specimen and cervicals of lemurs to raise the possibility that this element actually belongs to a lemuriform in the size range of *Varecia*. One basis for this conclusion is the width of the transverse

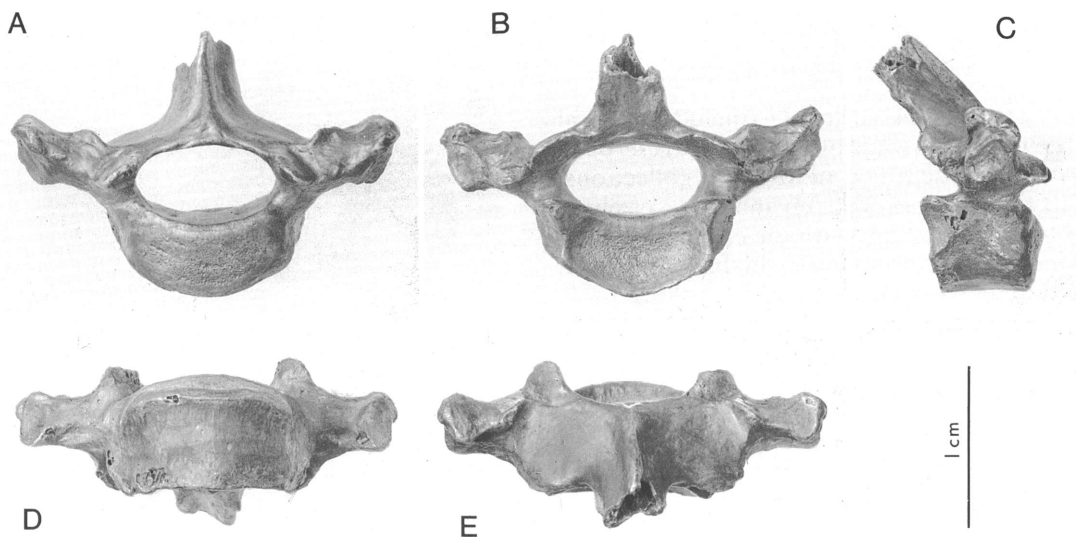


Fig. 13. An anterior thoracic vertebra, *Plesiorycteropus* sp. MNHNA 1987.043F. A, anterior; B, posterior; C, lateral; D, ventral; and E, dorsal views.

foramen, which is two to three times larger than the equivalent foramen in the atlas referred to *Plesiorycteropus*. Large transverse foramina are characteristic of lemurs; because the internal carotid is reduced, the circulus arteriosus receives most of its supply from the vertebral arteries (MacPhee and Cartmill, 1986). The internal carotid does not appear to have been reduced in *Plesiorycteropus* (see Morphology of the Cranium), and, in view of the small size of the brain in *bibymalagasy*, hypertrophy of the vertebral arteries would be unexpected. Accordingly, this element is not included in the hypodigm.

THORACIC VERTEBRAE

Seven thoracic vertebrae have been recognized in existing collections, six of which clearly belong to the anterior or middle part of the series and one to the posterior (table 9). Lamberton (1946) examined five specimens, but the only one figured (pl. IV, fig. 12, 12a) does not seem to precisely match any element in existing collections and is presumably lost.

The thoracics vary in size, but they all share some unusual details of centrum construction: (1) the bean-shaped articular surfaces for the intervertebral disks are much wider

transversely than dorsoventrally; (2) the intervertebral surfaces are moderately opisthocoelous (convex anteriorly, concave posteriorly); and (3) the centrum in lateral view is rhomboidal rather than rectangular in outline. These features are seen in their most exaggerated form in the lowest thoracics (and the lumbar), but even the anteriormost vertebrae in the thoracic series display attenuated versions of the same trait complex (e.g., fig. 13). Traits 2 and 3 are especially distinctive, although many mammals (including aardvarks, armadillos, and condylarthrans) display some degree of opisthocoely. Manids, however, do not (Emry, 1970).

MNHNA 1987.043F is a well-preserved anterior thoracic lacking only the tip of the spinous process (fig. 13). The centrum is short but broad, and displays a low midline carina on its ventral surface. The latter feature is variably expressed on other anterior and middle thoracics, but becomes very pronounced in the posterior thoracic/lumbar region (fig. 17). Other noteworthy features include robustly built transverse processes and a rather gracile spinous process. MNHNA 1987.043J (not illustrated here), the only definite posterior thoracic, is much larger than 1987.043F, suggesting that thoracic size increased caudad in *bibymalagasy* (a point that

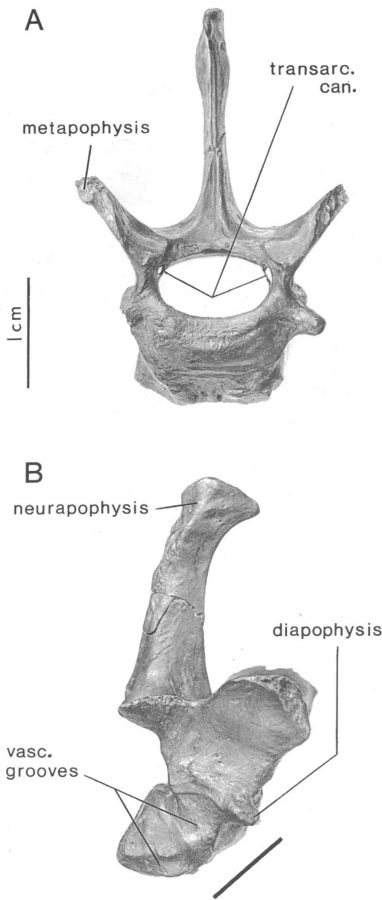


Fig. 14. An ?anterior lumbar or transitional vertebra, *Plesiorcyteropus* sp. MNHNP 515. A, anterior, and B, lateral views. Note asymmetry of transarcual canals and marked obliquity (line in B) of anterior intervertebral facet.

can be more securely made with the lumbar, q.v.). Although the centrum of this vertebra is well preserved, the processes arising from the neural arch are badly damaged. The centrum is incised by prominent vascular grooves. Because of their complexity, features related to the passage of blood vessels are separately treated, after description of the morphology of caudal vertebrae.

Prezygapophyses of bibymalagasy thoracic vertebrae do not bear specialized "embracing facets" of the sort described for manids by Emry (1970) and for *Arctocyon* by Russell (1964). The anterior and posterior epiphyseal surfaces of the centra are pitted (fig. 13A, B),

as in *Manis* and *Patriomanis* (Emry, 1970), but this is not a trait to which I am inclined to give any weight.

LUMBAR VERTEBRAE

The lumbar sample consists of the four associated specimens from *Ambolisatra* (MNHNP 540-543) and four others (MNHNP 515 and MNHNA 1987.043K-M) that closely agree with them in architecture (figs. 14-17). However, some features vary among specimens, which suggests to me that both species of bibymalagasy are probably represented in the sample.

The *Ambolisatra* specimens (fig. 17) help to clarify the probable number of elements in the lumbar region. The postzygapophyses of MNHNP 540 articulate well with the prezygapophyses of MNHNP 542, and the postzygapophyses of MNHNP 543 articulate just as well with the prezygapophyses of MNHNP 541. The fit between MNHNP 542 and 543 is good but not perfect. On this evidence, and assuming that there were no species differences in the number of lumbar vertebrae, we may conclude that *Plesiorcyteropus* had a minimum of four lumbar elements. However, I suspect that the actual number had to have been higher, at least five or six. Even higher counts, as in hyraxes and *Meniscotherium* (Williamson and Lucas, 1992), are possible in principle but unconfirmable with present evidence. Assuming that the *Ambolisatra* series represents one individual and arranging specimens in probable anteroposterior order (fig. 17), one can detect fairly regular clines in various morphological features (e.g., size and angulation of transverse processes, degree of development of the muscular process on the dorsal margin of the postzygapophysis, size and angulation of the spinous process). Further, the zygapophyses of the posterior thoracic (MNHNA 1987.043J) articulate tolerably well with MNHNA 1987.043K and L, here interpreted as Lu1s. As noted, the only morphological gap that cannot be easily closed with existing specimens is the one between MNHNP 543 and 542, which do not articulate as tightly as do other pairs. If MNHNP 542 represents Lu3, then 543 may be Lu5, the intervening vertebra having not been collected. This sug-

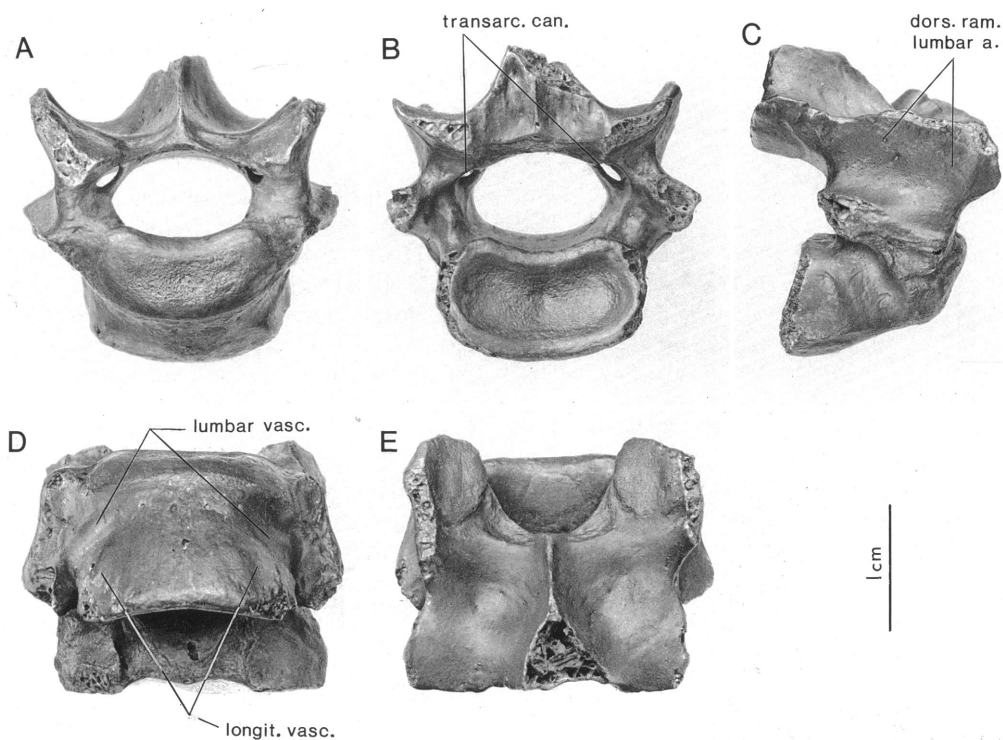


Fig. 15. An anterior (?2nd) lumbar vertebra, *Plesiorycteropus* sp. MNHNA 1987.043M. A, anterior; B, posterior; C, lateral; D, ventral; and E, dorsal views. Note large impressions for lumbar arteries and veins and intersecting longitudinal vasculature.

gests a total of six lumbar vertebrae, as depicted in figure 18. For convenience, these decidedly provisional identifications will be utilized in the following descriptions (see also table 9).

MNHNA 1987.043M and MNHNP 540, provisionally regarded as Lu2s, can be considered typical of the lumbar series (figs. 15, 17). As seen from the lateral aspect, the centrum is trapezoidal in shape, due to the anterior articular surface being markedly smaller than the posterior. The upper third of the centrum is deeply incised by grooves for lumbar vasculature. The apophyses of the neural arch are large and projecting. The transverse processes of Lu2 are angled sharply upward; in subsequent vertebrae they become somewhat more recumbent, wider, and longer, a common progression among mammals (Lestertisseur and Saban, 1967b). The mammillary processes (metapophyses) display the opposite trend, becoming smaller between Lu2

and Lu6. All of them, however, are well developed, implying that semispinalis, multifidus, and associated epaxial muscles were of significant size. The articular facets on the prezygapophyses become more concave and those on the postzygapophyses become more convex between Lu2 and Lu6, but the contrast between the upper and lower ends of the series is not very marked. As in the thoracic part of the column, the tongue-in-sleeve architecture of manid zygapophyses is definitely absent.

Two specimens retain intact neurapophyses—MNHNP 542, a provisional Lu6 (fig. 17, far left), and MNHNP 515, which I am unable to place more exactly than as an “anterior lumbar” (fig. 14). The Lu6 neurapophysis is notably long and gracile and leans slightly caudad. The centrum is squat and robust. Judging by their stumps, the neurapophyses of the other posterior lumbar were also long and gracile and probably oriented

subvertically. This specimen represents the last free presacral vertebra (highly probable because it is only fractionally too large to articulate with the sacrum, MNHNA 1987.043N), and I therefore emphasize that it lacks any sign of xenarthry.

MNHNP 515 (fig. 14) deserves special mention for several reasons. This element is clearly a transitional vertebra. I place it among the anterior lumbar vertebrae because the transverse process is very short and there are no rib facets. The large mammillary processes seen in this specimen presumably occur in the posterior thoracics and other anterior lumbar vertebrae, but in the available specimens they are sheared off. Yet it is necessary to note that, in a few respects, MNHNP 515 strongly recalls the last *cervical* of some artiodactyl groups (especially bovids). In bovids, the seventh cervical differs markedly from both the other cervicals and the anterior thoracics in the following regards: (1) dome-shaped anterior articular surface is strongly sloped; (2) lobular transverse processes lack transverse foramina (which are shifted to a more medial position and communicate with the vertebral canal); (3) prezygapophyses possess flaring "pseudomammillary processes" (pseudometapophyses); (4) intervertebral notch is broadly open, not confined as in thoracics; and (5) tip of long neurapophysis is retroflexed rostrad. Each of these features is encountered in MNHNP 515. Against attributing this vertebra to the cervical part of the column may be listed the very large size of the centrum, with vascular markings consistent with the lumbar region. Even more important, MNHNP 515 exhibits the vascular canals situated *inside* the neural canal that are also seen in definite posterior thoracics and lumbar vertebrae (see below).

MNHNP 515 is clearly an unusual vertebra, and nothing quite like it occurs in any of the extant members of the comparative set. Xenarthrans can be discounted, and in *Orycteropus*, *Manis*, and *Procyon* the first lumbar and seventh cervical are not highly differentiated from the vertebrae with which they articulate. Vertebrae of *Meniscotherium*, *Hyopsodus*, and *Ectoconus* (Gazin, 1965, 1968; Matthew, 1937) and other primitive ungulates are generally very poorly described and illustrated in the literature, but so far as

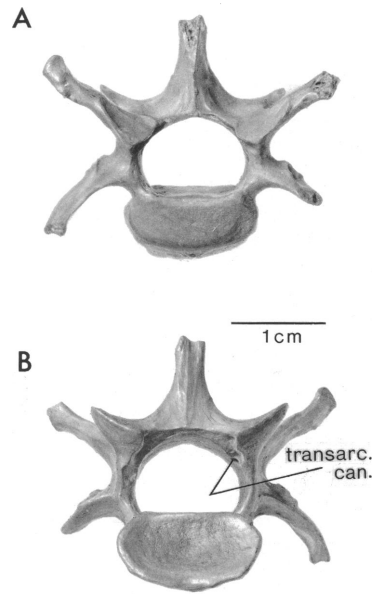


Fig. 16. A third (?) lumbar vertebra (MNHNP 542) attributed to *Plesiorhycteropus madagascariensis*. A, anterior, and B, posterior views. Only one transarcual canal is visible.

I can judge there seems to be no vertebra answering to the description of MNHNP 515 at the cervicothoracic or thoracolumbar transitions in these taxa.

If the Ambolisatra sample is representative, a very remarkable feature of the bibymalagasy lumbar region is progressive caudad reduction in the anteroposterior width (NAW) of the laminae of the neural arches (figs. 17, 18; table 9). This style of arch diminution has no good parallel in the comparative set and is very rare in eutherians overall (see Function, Adaptation, and Extinction). Another feature of the Ambolisatra sample is that lumbar centra decrease in anteroposterior length (CO, CL) while increasing in mediolateral breadth (PIT). Progressive caudad shortening and widening in centra of posterior lumbar vertebrae is also a very uncommon trait (Lessertisseur and Saban, 1967b), although among the taxa of interest here it is found in the primitive ungulate *Meniscotherium* (Gazin, 1965). The significance of these features is reviewed in a later section (see Function, Adaptation, and Extinction).

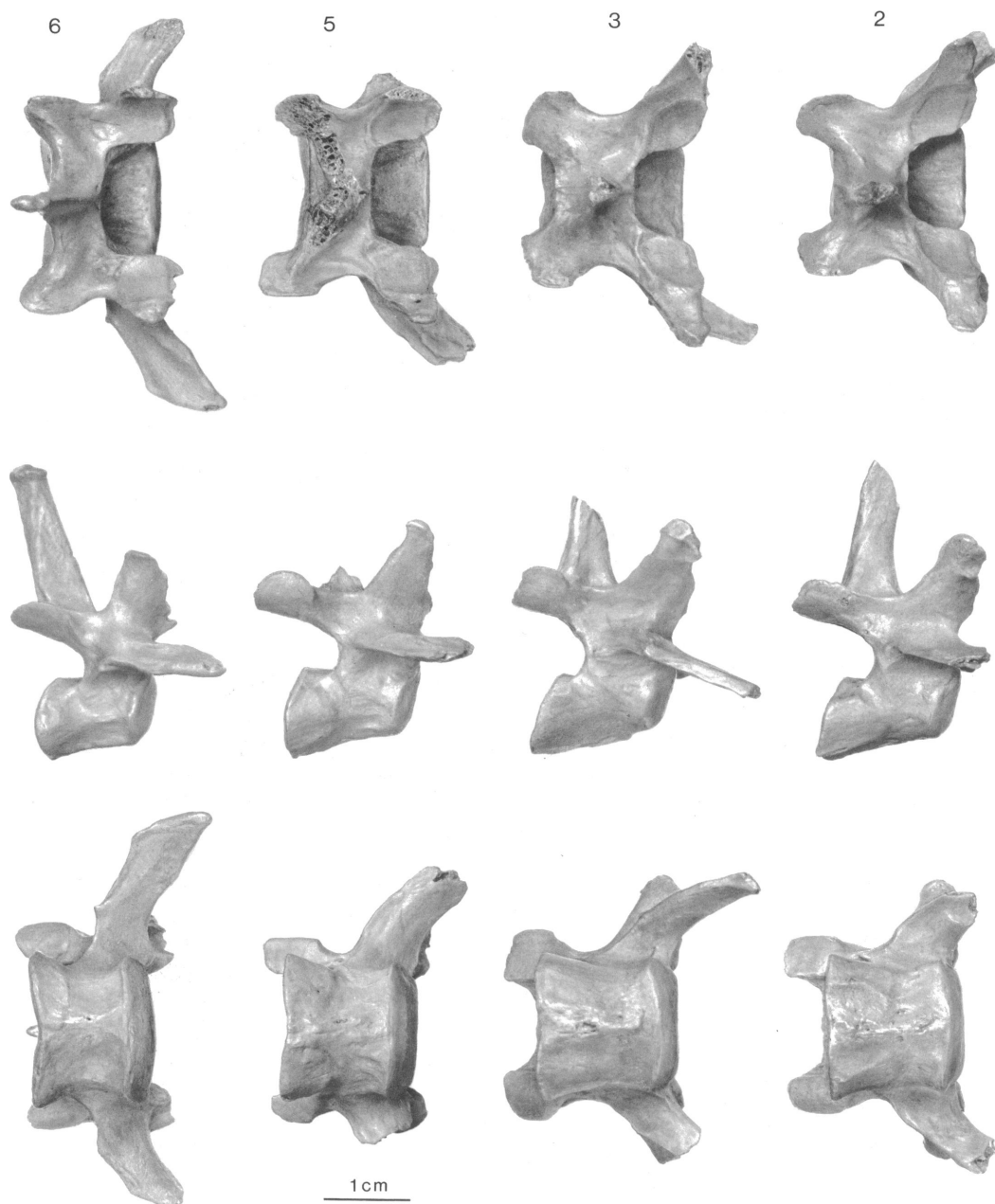


Fig. 17. Associated lumbar vertebrae from *Ambolisatra* (MNHNP 540-543) attributed to *Plesiorycteropus madagascariensis*, in dorsal (**top**), right lateral (**middle**), and ventral (**bottom**) views.

SACRUM

The partial sacrum from Ampoza now cataloged as MNHNA 1987.043N (fig. 19) is evidently not the same as the complete specimen (now lost) from *Ambolisatra* described

by Lamberton (1946). However, for comparable features the Ampoza specimen agrees with Lamberton's (1946) description and may therefore be validly assigned to *Plesiorycteropus*.

The *Ambolisatra* sacrum consisted of sev-

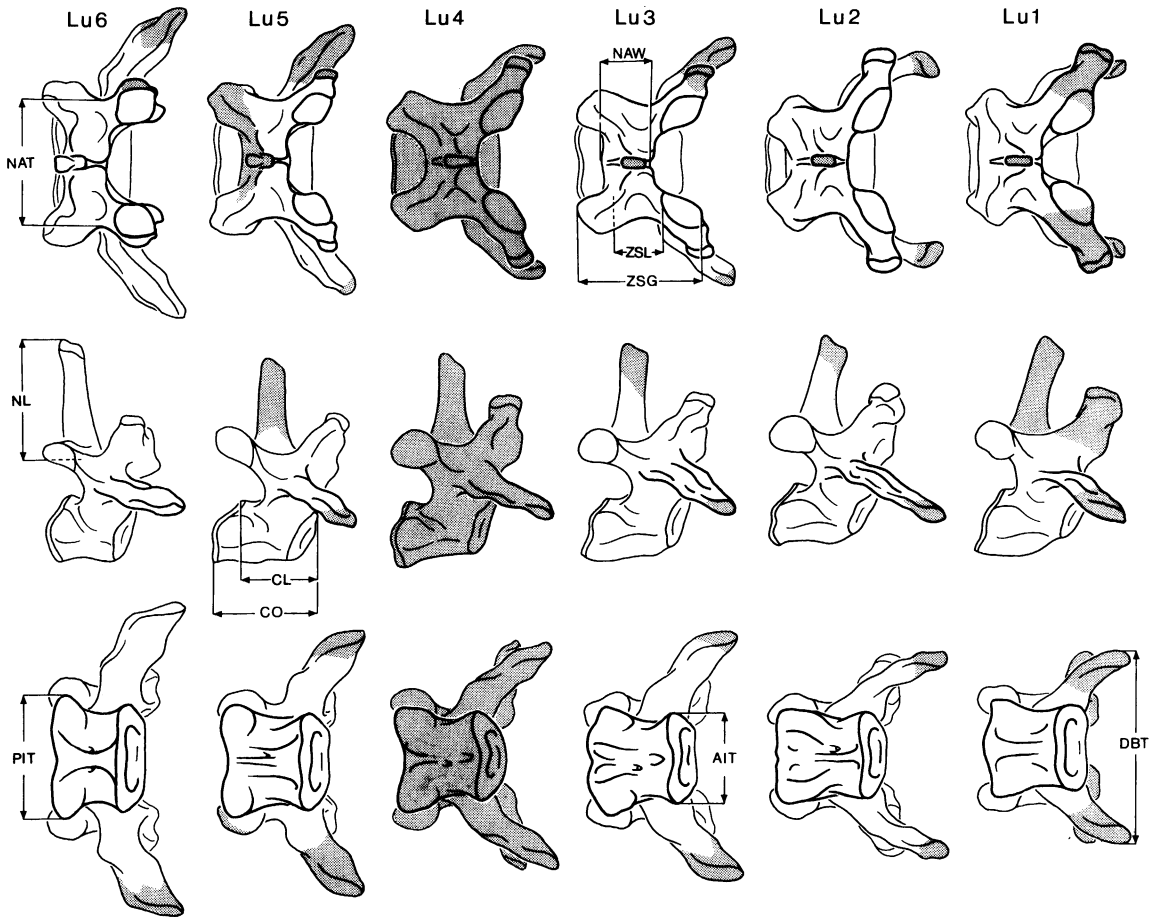


Fig. 18. Reconstruction of lumbar series of *Plesiorycteropus* in dorsal (**top**), right lateral (**middle**), and ventral (**bottom**) aspects, with the assumption that bibymalagasy possessed six lumbar vertebrae. Reconstructions are largely based on associated elements from *Ambolisatra* (see text); missing structures indicated by stipple. See table 9 for measurement acronyms. Note in particular that transverse width of centra (PIT) increases posteriorly while neural arch width (NAW) decreases in same direction.

en fused elements (Patterson, 1975), but the incomplete Ampoza specimen preserves only the first two sacrals and a portion of the third. The prezygapophyses of Sa1 are too abraded to warrant description. The promontory is intact and moderately inclined toward the ventral. The articular surface of the promontory is strongly convex, indicating that the last lumbar's posterior articular surface was correspondingly concave. Only the first two sacrals participate in the sacroiliac joint; contra Lamberton (1946), there was no sacroiliac fusion (cf. Patterson, 1975). Judging from Lamberton's figures of the *Ambolisatra* specimen (see fig. 32), there was obviously very close approximation of sacral transverse pro-

cesses and the inner aspect of the ischium, as seen in aardvarks, manids, and vombatids among other mammals. However, there was just as clearly no true sacroischial fusion of the sort seen in almost all xenarthrans, many moles, and a few other mammals (see Pelvic Girdle and Hindlimb, Innominate).

An outstanding feature of the bibymalagasy sacrum is the great transverse separation of the prezygapophyses of Sa1 (table 9; fig. 19C). Lamberton (1946), who noted this trait, stated that prezygapophyseal separation in *Plesiorycteropus* was almost as great as in *Orycteropus afer*, a much larger animal. While his statement is somewhat of an exaggeration, the progressive increase in the distance be-

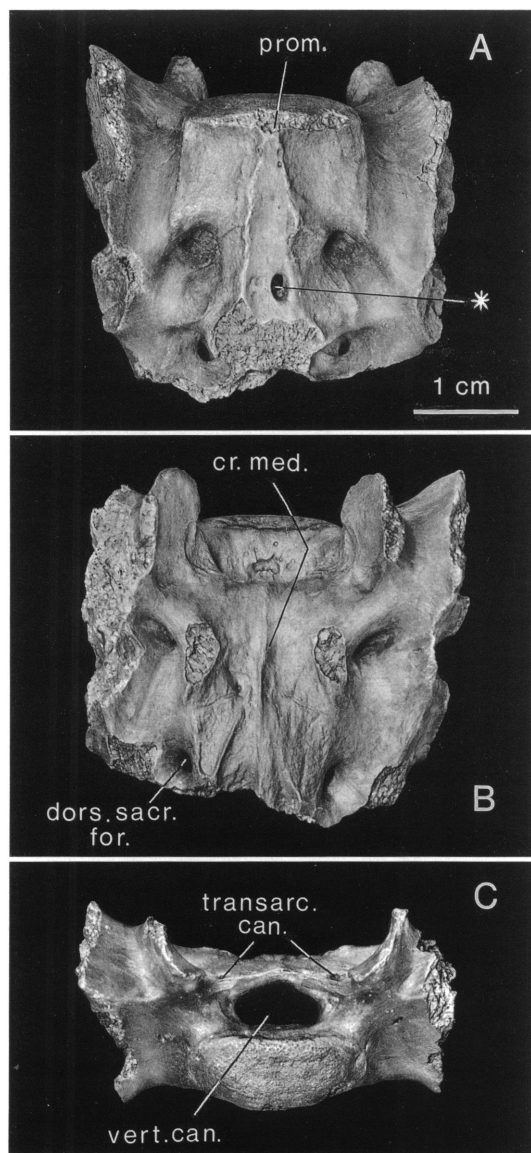


Fig. 19. Sacrum, *Plesiorycteropus* sp. MNHNA 1987.043N. A, ventral; B, dorsal; and C, anterior views. Asterisk in A points to foramen of unknown function that leads into vertebral canal; may be associated with vasculature running through transarcual canals.

tween the zygapophyses seen in the posterior lumbar is very noticeable and obviously continued up to the lumbosacral joint (see Function, Adaptation, and Extinction).

According to Lamberton (1946), the first

sacral lacks a distinct neurapophysis, its position being marked only by a very low mid-line ridge. This ridge is also present in MNHNA 1987.043N. In the *Ambolisatra* specimen the neurapophyses of the succeeding sacra were distinct and became progressively more vertical and robust caudad. The tips of S5-7 of the *Ambolisatra* specimen were fused at their dorsal tips and evidently formed a narrow platform (fig. 32).

The sacrum of *Orycteropus*, usually consisting of six or seven elements (fig. 32), is similar to the foregoing in several respects (also cf. Lönnberg, 1906). Only the first two sacra and a small part of the third are involved in the sacroiliac articulation, which is restricted to the middle part of the ilium. The sacral neurapophyses increase in size caudad, although the first is actually more prominent than the second or third. The neurapophyses form a continuous, fused ridge, although the tips of the posterior ones are discrete and do not form a dorsal platform. The metapophyses are low but distinct and the lateral margins are slightly upturned, although less so than in *Plesiorycteropus*. Contrasts include the lack of strong muscular markings for tail flexors on the ventral surface and the much narrower costal processes of the last pseudosacral. Condylarthrans had relatively short sacra (*Meniscotherium*, 4 elements; *Phenacodus*, 3 to 5 elements [Gazin, 1965]). Patterson (1975: 231) argued that the tubulidentate sacrum could easily be derived from that of an animal like *Meniscotherium* by incorporation of anterior caudals, but provided no reasons why this transformation should be regarded as more reasonable than any other.

Manids (fig. 32) differ considerably from *Plesiorycteropus*. There are only three to five sacral elements; all participate in the sacroiliac joint, so that the auricular surface extends all the way to the position of the ischial spine. Neurapophyses and metapophyses are large and nearly of equal size, and form three strongly-projecting parallel rows along the dorsal aspect of the sacrum. Fusions across the tips of both metapophyses and neurapophyses are frequent but variable in position. The costal elements of the last sacral are strongly built, but their tips are swept high above the level of the ischial tuberosity. Myr-

mecophagids have many of these same features and are thus also quite different from *Plesiorhycteropus*. Dasypodids also appear to be quite different, although this is partly conditioned by the number of elements (8 to 13) and massive fusion of terminal sacra to the sciatic margins of the ischia (fig. 32). Hyraxes have multielement sacra (7 to 9 elements; Le Gros Clark and Sonntag, 1926), but their widths sharply decrease caudally. Only the first sacral is significantly involved in the sacroiliac articulation, although the second sacral may make a small contribution as well. Neurapophyseal development is negligible.

In lipotyphlans, sacra tend to be short except in the digging moles. Among taxa with more generalized sacra, *Echinosorex* (fig. 32) is similar to *Plesiorhycteropus* in having a square rather than triangular sacrum, with the last sacral having notably broadened transverse processes that nearly touch the ischia. However, the similarity can scarcely be called detailed in any other regard. Neurapophyses are not usually fused together; even when they are, as in some erinaceids (Frost et al., 1991), their tips are not expanded to form a platform.

CAUDAL VERTEBRAE

Patterson (1975) maintained that Lamberton (1946) misidentified caudal vertebrae as lumbar, but his statement to this effect seems to have been based on Lamberton's mislabeling of two figures (Lamberton, 1946: pl. IV, figs. 13 and 14). In fact, Lamberton's text establishes that he was aware of the morphological differences between lumbar and caudals and he described both types of vertebrae accurately. Another figure (pl. IV, fig. 15) on the same plate as the mislabeled caudals may depict a definite lumbar (though identified as a postsacral), but the reproduction is too poor for certain identification.

The set of five associated caudals from Ambolisatra (MNHN 1714-1718) can be readily articulated in a plausible anterior-posterior sequence (fig. 20). Their size, well-separated zygapophyses, and large neural canals indicate that they came from the anterior part of the tail region, which must have been proportionately massive. Interestingly, the

articular surfaces of the centra continue the same trend (marked opisthocoely) seen in the presacra. There are evident facets for hemal arches, although no hemal elements have been found in collections.

In addition to caudals with barlike transverse processes that arise from the centro-lateral aspect of the centra, there are two specimens (MNHN 1987.087S, T) placed with the *Plesiorhycteropus* sample that are somewhat different. Their transverse processes are shorter, arise from the entire lateral aspect of the centrum, and are perforated by large vascular canals. These elements are clearly from a more caudal position in the tail, but, in view of their large size, and if properly attributed, they must have been followed by still others.

The tail vertebrae of *Orycteropus* differ in that only the first two or three have large, flat, transverse processes that emerge from their centra at approximately a right angle. In the next 14-16 caudals, the transverse processes become progressively shorter, more barlike, and more acutely angled and caudally displaced on the centrum. Manid anterior caudals bear well-developed transverse processes similar in size and shape to those of *Plesiorhycteropus*, but there is much less heterogeneity among elements. The tails of smaller pangolins are prehensile, capable of suspending the entire weight of the body (Kingdon, 1974). However, well-developed transverse processes are not found in the distal part of the tails of prehensile-tailed New World monkeys, which tends to imply that they are not strictly necessary for strong rotatory motions of the tail. In the absence of any positive evidence for tail prehensility in *Plesiorhycteropus*, there appears to be no good reason to impute it.

VASCULAR FEATURES

The posterior portion of the bibymalagasy vertebral column (i.e., the section extending from the midthoracic area to the upper part of the caudal region) exhibits two kinds of features, related to the passage of blood vessels, that deserve special comment—(1) grooves for intersegmental vessels on vertebral centra; and (2) longitudinal canals within

the neural arches, apparently for large venous sinuses.

GROOVES FOR INTERSEGMENTAL VESSELS

Lamberton (1946: 33 [trans.]) was much impressed by large, symmetrically positioned vascular grooves on the lumbar centra of *Plesiorhycteropus*: his description of these grooves is set off from the rest of his text in italics, and is accompanied by the declaration that their incidence "ought to be investigated in collections in the possession of the great museums, because [they] might put us on the track of the possible affines of the enigmatic Malagasy fossil."

Vascular grooves on vertebral centra are not nearly so rare as Lamberton (1946) appears to have thought, although those of *Plesiorhycteropus* are unusually well marked. Among other taxa, grooves on vertebral centra occur in *Orcyteropus*, *Solenodon*, *Tenrec*, *Priodontes*, *Metacheiromys*, *Pantolambda*, and *Ectoconus*, and they may well be primitive for Eutheria. In *Plesiorhycteropus*, grooves are found on most elements in the posterior thoracic, lumbar, and caudal vertebral regions. Grooves are best developed in the posterior thoracic/anterior lumbar region and anterior caudals (figs. 14, 15, 20). They are faint or nonidentifiable on the few anterior/middle thoracic elements available (fig. 13). They become progressively smaller through the lumbar series and disappear on the sacrum, but reappear on anterior caudals.

Lamberton (1946) did not attempt to determine the homology or content of these grooves, although it seems reasonable to believe that they carried divisions of intersegmental arteries and veins. Some fine details of vascular organization in the lumbar area are worth exploring here, however, in order to appreciate the possible function of the transarcual canals (see below).

In *Homo* (Warwick and Williams, 1973), and no doubt in mammals generally, lumbar arteries arise from the posterolateral aspect of the dorsal aorta, directly ventral to lumbar centra. To reach the lateral and dorsal parts of the body wall, each lumbar artery travels around its related centrum toward the ipsilateral intervertebral foramen. At the foramen, the artery normally bifurcates into a

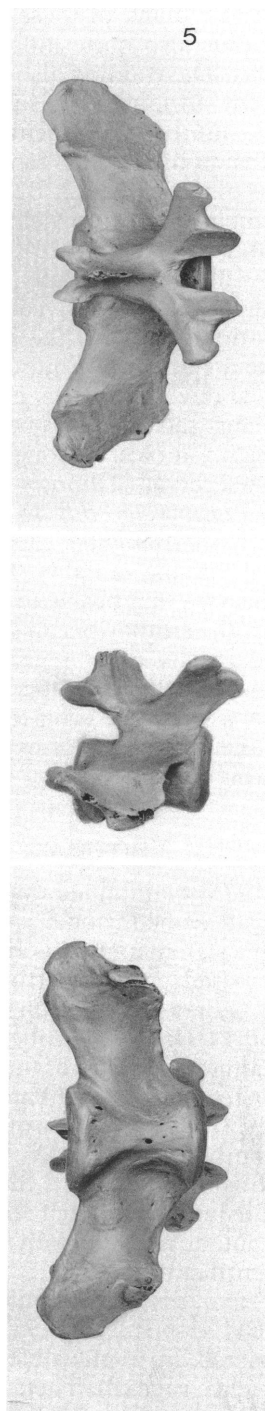


Fig. 20. Associated anterior caudals from Am-bolisatra, attributed to *Plesiorhycteropus madagascariensis* (MNHNP 1714-1718), in dorsal (top), right lateral (middle), and ventral (bottom) views.

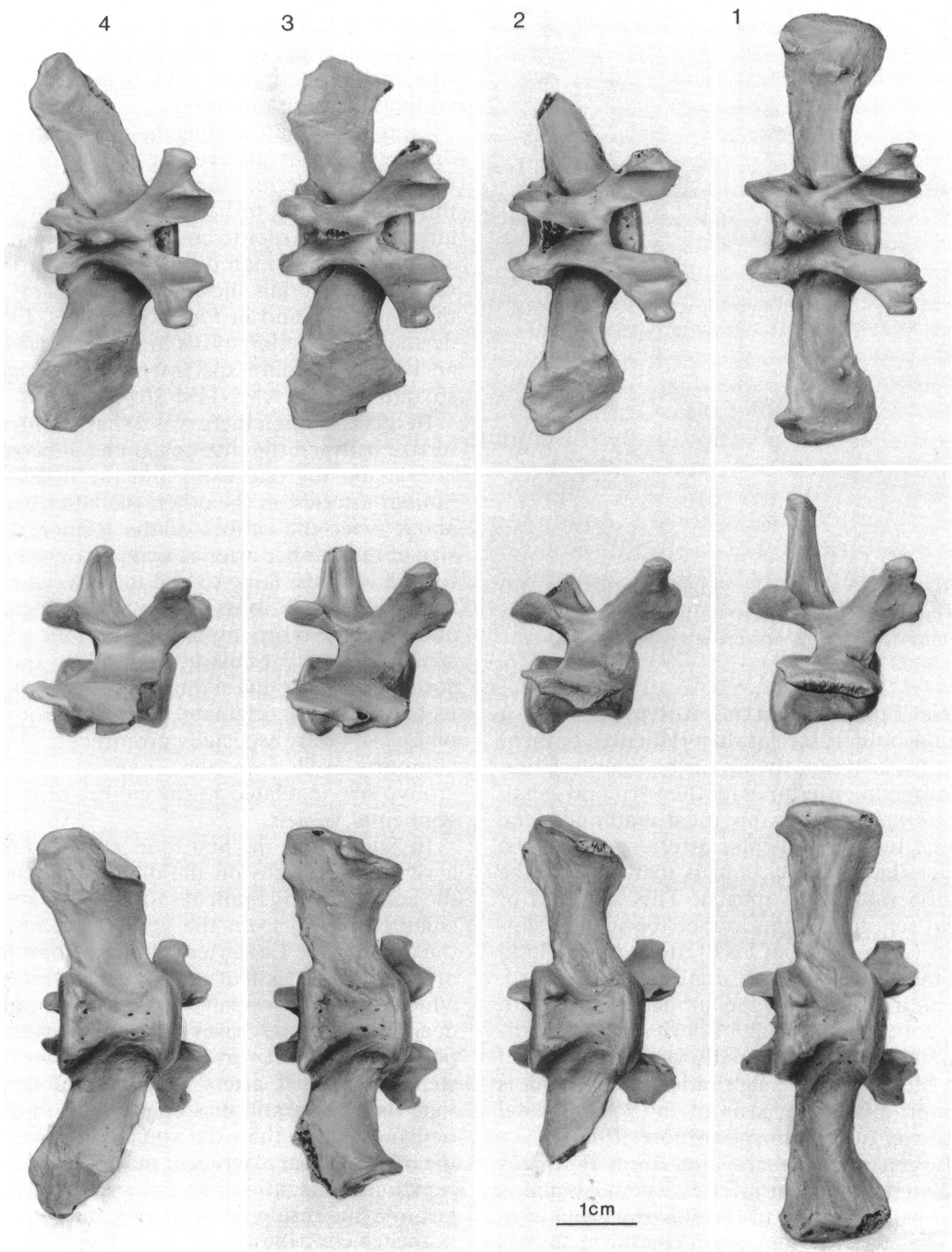


Fig. 20 (continued)

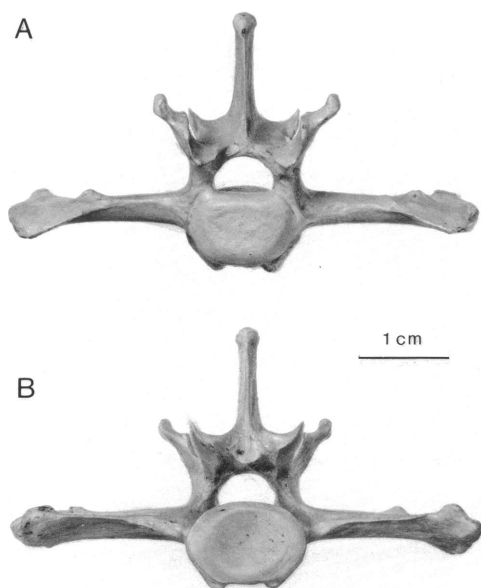


Fig. 21. An anterior caudal (MNHNP 1714) attributed to *Plesiorycteropus madagascariensis* in A, anterior, and B, posterior views.

dorsal ramus to epaxial musculature and a spinal branch (or lumbar radicular branch) that twists under the lip of the intervertebral foramen in order to enter the vertebral canal. In *Homo* and probably most mammals, one of the lumbar radicular arteries tends to be larger than the rest, and is identified as the arteria radicularis magna. This vessel is of great functional importance, because it supplies (in humans, at least) most of the blood for the posterior two-thirds of the spinal cord, including the area of the lumbar enlargement. By contrast, radicular arteries in the mid-thoracic area are normally very small, and if the blood flow through radicularis magna is compromised, necrosis of the lower spinal cord can quickly ensue (Moore, 1987).

In general, lumbar veins drain the areas irrigated by lumbar arteries; venous blood is normally returned to the superior vena cava by the azygos system, although other routings are possible. The dorsal aorta and the collectors for the azygos system are prevertebral in position, lying ventral to the plane of the vertebral column as a whole. Thus each ipsilat-

eral pair of intersegmental vessels must wind across the corresponding vertebral centrum in order to reach their destinations, and it is this part of their track that is indicated by grooves in some mammals.

Lipotyphlans are among the mammals that display vascular grooves on posterior thoracic and anterior lumbar vertebrae (although they tend to be well marked only in large taxa). In order to confirm that relations as seen in the human occur in a similar format in a eutherian showing at least some of the features found in *Plesiorycteropus*, I undertook a dissection of the lumbar arteries of an injected alcohol specimen of *Solenodon* sp. (adult male, AMNHM 20197).

In this specimen there was a sharp contrast in size between the intercostal and subcostal arteries on the one hand and the first four lumbar arteries on the other, the latter being about twice the caliber of the former. The size of the lumbar arteries appears to be correlated with the large size of the epaxial and hypaxial muscle mass in the pelvic region, and, possibly more important, with the great size of the lumbar enlargement of the spinal cord, where the rami of the lumbosacral plexus anatomically originate. Vascular grooves on Lu1–L4 were especially prominent, which comports well with the supposition that groove size is related to the caliber of intersegmental vessels.

In *Solenodon*, the first four lumbar form a very large plexus on the dorsal surface of the aorta, sending branches to the psoas musculature arising from the ventral aspects of the centra. The Lu4 artery shares a common origin with the testicular artery. Dorsal rami, which descend caudally from their origin, deeply crease the bases of the prezygapophyses of the next vertebra in the series. The stem of the Lu1 artery is somewhat larger than its fellows, and its spinal branch in particular is larger than the spinal branches of the other lumbar arteries. It may therefore be functionally identified as the arteria radicularis magna. Inside the vertebral canal, spinal branches contribute to a very large midline artery which is apparently equivalent to, but comparatively much larger than, the "central anastomotic chain" of *Homo* (cf. Warwick and Williams, 1973). This midline artery,

which is situated on or in the dura mater ventral to the lumbar enlargement of the spinal cord, can be traced down into the sacrum and up into the thoracic part of the spine, but its caliber diminishes in both directions.

Turning now to the specific conditions found in *Plesiorhycteropus* (fig. 17), we find that grooves attributable to intersegmental vessels are situated in expected positions: they originate on either side of the midline of the centrum, and run upward and backward to the intervertebral notches. Extremely well-marked impressions for intersegmental vessels are seen on lower thoracic and upper lumbar vertebrae. The impressions are less strong on Lu4 and Lu5. The depth of grooving probably reflects hypertrophy of both arteries and veins, although other evidence discussed below may indicate that only the veins were enlarged. The deepest groove for a dorsal ramus was seen on the pedicle of a putative Lu2 (fig. 15). If the arrangement of divisions was as it is in *Solenodon*, this dorsal ramus would have originated from the lumbar artery of the preceding vertebral element, i.e., Lu1. This may imply that the Lu1 artery was hypertrophied and provided the largest radicular artery, as in *Solenodon*.

Elements in the posterior thoracic/anterior lumbar section of the midaxial region display an additional feature, possibly but not definitely vascular in origin. The centra of the vertebrae in question exhibit bilateral longitudinal grooves that seem to terminate in, or at least to overlap, the horizontal grooves believed to have carried the trunks of the intersegmental arteries and veins (fig. 15). The grooves are reasonably distinct and do not appear to relate to muscular or ligamentous attachments. I know of no reports that describe similar features in any other mammals. If they are indeed vascular impressions, they must represent tracks for longitudinal venous channels, if only because mammals do not possess dual dorsal aortae in the adult stage. The plexus produced by anastomotic twigs from the lumbar arteries of *Solenodon* does not reside in identifiable channels on vertebral centra, so it is unlikely that such a plexus, if formed in *Plesiorhycteropus*, could have been responsible for these features in bibymalagasy.

LONGITUDINAL CHANNELS IN NEURAL ARCHES

In addition to vascular grooves on vertebral centra, bibymalagasy also possessed enclosed longitudinal channels in the neural arches of the posterior free vertebrae (figs. 14–16; C 19). Neither Lamberton (1946) nor Patterson (1975) made any reference to these channels, which I will refer to as “transarcual canals” (from *arcualis*, L., pertaining to an arch; so named because they penetrate the inner aspect of the laminae of the neural arches). These canals are positioned differently from, and are therefore apparently not the homologs of, “emissary” channels seen on the dorsal side of lumbar neural arches (e.g., *Macaca*, *Thylagale*), transverse processes (e.g., *Tamandua*), pedicles (e.g., lorisiforms, suiforms), and elsewhere (Flower, 1885; Barnett et al., 1958).

Transarcual canal occurrence/size (TFS) in the bibymalagasy vertebral sample is presented in table 9. The largest apertures are found in the posterior thoracic/anterior lumbar region. They diminish in size both anteriorly and posteriorly, being mere pinholes in the midthoracics as well as in the lower lumbar and the first sacral. No apertures were observed in the caudal vertebrae. Several vertebrae were asymmetrical in having canals of conspicuously different widths, or in having only one, always very small, transarcual canal (e.g., fig. 14). In these last cases the canal was sometimes nonperforating, i.e., it ended within the substance of the neural arch. Numerous small holes occur on the walls of the complete canals, evidently for tiny vessels entering from the spongiosum.

To my knowledge the occurrence of transarcual canals has not been heretofore noted in mammals except in the form of incidental references (e.g., nonspecific foramina in thoracic neural arches of *Bos taurus*; Sisson and Grossman, 1938). Stromer (1902: 68) referred to pedicular canals in upper thoracics of *Mustela putorius* and occasional perforations in *Lycaon pictus*. However, I find that in *M. putorius* the canals described by Stromer also occur in the last cervical, and, moreover, these canals are in line with the transverse foramina of cervicals 1–6. While these

TABLE 9
Plesiorhynchus: Measurements of Postcervical Vertebrae (in mm)^{a,b}

Specimen no.	Region	CL	CO	DBT	AIW	AIT	PIW	PIT	VCW	VCT	NL	NAW	NAT	ZSG	ZSL	TFS
MNHNA 1987.043D	Ath	6.6	7.0	26.5	4.4	9.3	4.9	8.8	4.4	8.0	—	5.2	14.5	9.7	4.7	NA
MNHNA 1987.043E	Ath	7.0	7.4	27.2	5.0	10.0	5.2	9.2	5.0	8.9	—	5.8	15.6	10.1	4.5	NA
MNHNA 1987.043F	Ath	7.1	7.3	23.6	5.1	9.6	5.6	9.8	5.5	8.6	—	7.0	13.1	11.0	4.7	NA
MNHNP 1652	MTh	9.0	9.4	21.4	5.4	10.5	5.8	11.1	5.1	8.2	—	—	12.7	13.3	4.6	NA
MNHNA 1987.043G	MTh	—	—	23.0e	—	—	—	—	5.3	8.4	—	7.1	7.2	12.3e	4.5	+1
MNHNA 1987.043H	MTh	9.0	9.8	—	4.8	11.3	5.2	10.7	5.4	8.4	—	—	—	—	—	+1
MNHNA 1987.043J	PTh	11.8	12.5	22.3e	5.5	13.2	7.6	14.3	6.9	8.9	—	8.9	6.9	19.0e	6.5	++++
MNHNP 515	Lu(?)	11.2	11.9	22.0e	5.8	14.0	7.4	13.5	6.0	9.3	23.8	9.1	16.1	17.0	5.1	++++
MNHNA 1987.043K	Lu(1)	12.1	13.3	—	6.4	12.4	7.6	14.0	7.7	10.3	—	9.0	15.8	—	7.5	++++
MNHNA 1987.043L	Lu(1)	11.7	14.0	—	5.7	13.5	7.4	14.0e	6.5	8.5	—	9.5	16.6	—	9.0	++++
MNHNA 1987.043M	Lu(2)	13.8	16.5	—	7.0	14.1	8.3	15.9	8.3	10.0	—	9.6	17.3	—	7.7	++++
MNHNP 540	Lu(2)	14.0	17.9	38.5e	7.2	15.2	9.1	16.5	9.2	12.5	—	8.9	17.3	20.7	7.3	++++
MNHNP 542	Lu(3)	14.5	18.9	—	7.7	15.6	9.6	16.9	8.5	12.5	—	8.6	18.0	21.0	5.5	++
MNHNP 543	Lu(5)	13.9	17.0	—	8.5	16.2	9.5	17.6	7.6	12.3	—	7.5	18.8	21.0e	2.5	+
MNHNP 541	Lu(6)	12.4	15.2	52.0e	8.5	17.3	9.7	18.9	7.5	12.3	18.7	6.1	22.9	20.6	1.7	+1
MNHNA 1987.043N	Sa1	NA	NA	36.0	7.7e	17.2	NA	NA	4.6	10.9	<1.0	NA	NA	NA	NA	+
MNHNA 1987.043N	Sa2	NA	NA	30.0	NA	NA	NA	NA	4.3	7.1	—	NA	NA	NA	NA	NA

^a General Abbreviations: Ath, anterior thoracic; MTh, middle thoracic; PTh, lower thoracic; Lu, lumbar (estimated position in parentheses); Sa1, 2, first and second sacral; e, estimate (made only if small area missing or mirror image of measurement point can be reconstructed); NA, not applicable; sp, in midsagittal plane; tp, in transverse plane.

^b Abbreviations and Definitions of Measurements:

CL Centrum, anteroposterior dimension. Between margins of anterior and posterior articular surfaces, measured along dorsal wall of centrum (sp).
CO Centrum, oblique dimension. Dorsal margin of anterior articular surface to ventral margin of posterior articular surface (sp). (Because of strong obliquity of articular surfaces in lower thoracic and lumbar regions, a single measure of anteroposterior centrum length cannot be satisfactorily defined.)

DBT Diapophyses (transverse processes), bitransverse dimension. Between lateralmost tips of transverse processes.

AIW Intervertebral articular surface, anterior; dorsoventral dimension. Dorsal to ventral margin (sp).

AIT Intervertebral articular surface, anterior; transverse dimension. Between lateral margins (tp).

PIW Intervertebral articular surface, posterior; dorsoventral dimension. Dorsal to ventral margin (sp).

PIT Intervertebral articular surface, posterior; transverse dimension. Between lateral margins, at right angle to PIW (tp).

VCW Vertebral canal, dorsoventral dimension. Maximum dorsoventral separation of rims of canal (sp).

VCT Vertebral canal, transverse dimension. Maximum separation of rims, at right angle to VCW (tp).

NL Neurapophysis (spinous process), maximum length. Dorsal rim of vertebral canal to tip of neurapophysis (sp).

NAW Neural arch, anteroposterior dimension. Anterior to posterior margins (sp).

NAT Neural arch, minimum transverse dimension. Between laminar (pedicular) margins as seen in dorsal aspect, at position of maximum constriction.

ZSG Zygapophyses, maximum ipsilateral separation. Anterior margin of prezygapophysis to posterior margin of postzygapophysis.

ZSL Zygapophyses, minimum ipsilateral separation. Closest approximation between facets of pre- and postzygapophyses. Anterior margin of postzygapophyseal facet to posterior limit of the prezygapophyseal facet. (Since facets face in opposite directions, both margins cannot be seen at once.)

TFS Facing one facet, transfer margin of other facet to observer's side (as though bone were transparent), and measure.

Transarcual foramina, relative size. Number of "+" signs indicates relative size of foramina (size of the larger foramen, in cases of asymmetry);

"++1" means very small, foramen on one side only.

canals ought to be investigated to see what their relationship is to vertebral arteries, they are seemingly not related to transarcual canals, which occur only at the caudal end of the thoracic series and in the lumbar. In camels and the litoptern *Macrauchenia*, the foramina transversaria of most of the post-atlantan cervicals are repositioned in such a way that they actually pierce the walls of the vertebral canal (Owen, 1840). Once again, however, canals of this sort are exclusively confined to the cervical region. Phocid seals display highly modified venous drainage patterns in the vertebral region (Ronald et al., 1977), but these alterations are not correlated with any obvious osteological features. Transarcual canals are not mentioned even in detailed works on cetacean vertebral anatomy (De Smet, 1977; Barnett et al., 1958) and therefore I assume that they are absent in whales and dolphins. Lorisine primates possess transpedicular foramina (W. C. O. Hill, 1947), and in *Loris* there can be an "accessory opening" of the transpedicular foramen that opens into the vertebral canal. Its position is quite different, however, from that of the transarcual canal as defined here.

My admittedly incomplete survey of mammals suggests that true transarcual canals are rather uncommon. Even in the few instances in which they have been found, in relative terms they are rarely as large as in *Plesiorycteropus* (table 10). Soricomorph lipotyphlans are the only identified major taxon in which large transarcual canals resembling those of *Plesiorycteropus* occur with some frequency. The strongest expression seen to date occurs in the two West Indian genera *Solenodon* and *Nesophontes* (fig. 22B). In investigated specimens of the Puerto Rican species *N. edithae*, the canals completely perforated neural arches, as they do in *Plesiorycteropus*. In the dissected *Solenodon*, these canals were rarely bilaterally symmetrical and transmitted veins only, not arteries or nerves. Because the venous system of the latter specimen had not been adequately injected, I could not determine how the transarcual vessels were related to the general pattern of venous drainage. However, my impression is that they are at least partly and perhaps mainly concerned with interior drainage of the vertebrae themselves. This would explain why they often

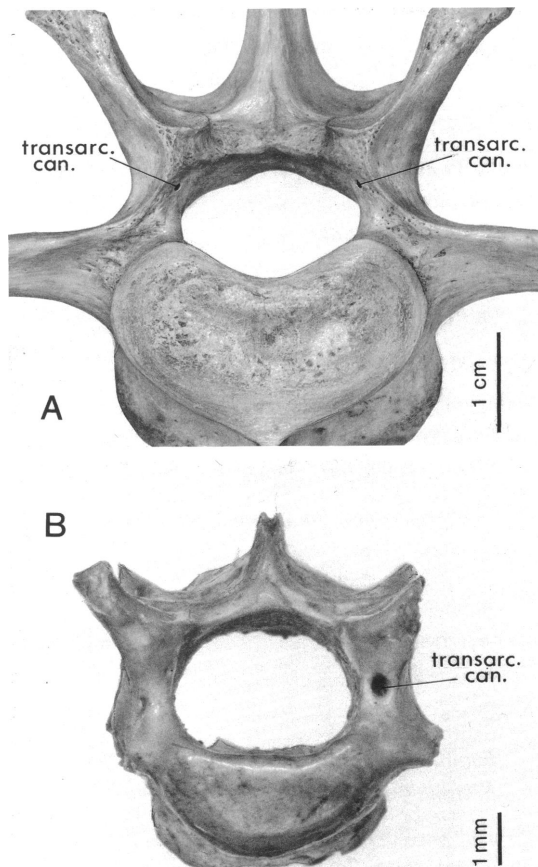


Fig. 22. Transarcual canals in a tubulidentate and an insectivore (note difference in size as indicated by scale bars). **A**, *Orycteropus afer* AMNHM 51235, anterior view of fourth lumbar vertebra, showing small foramina in the position of transarcual canals. The foramina are nonperforating (i.e., they do not continue through to the posterior surface of the neural arch). **B**, *Nesophontes edithae*, anterior view of unaccessioned lumbar vertebra in AMNHP collections. This extinct Antillean soricomorph has prominent, perforating transarcual canals, as does its extant relative *Solenodon*. In this specimen, only one side has a patent canal; asymmetry in canals is also seen in *Plesiorycteropus*.

seem to end blindly, within the substance of the neural arch. This does not preclude the possibility that they are also connected with the drainage of plexuses around the spinal cord, but this remains to be demonstrated in suitable material. Transarcual canals of moderate size were also found in the chryso-

TABLE 10
Incidence of Transarcual Canals in Mammals^a

	Incidence	Condition
Condition in <i>Plesiorycteropus</i> :	post. thoracics, lumbar, sacral 1	all large, perforating
Similar to <i>Plesiorycteropus</i> :		
Lipotyphla		
<i>Nesophontes edithae</i>	post. thoracics and lumbar?	examples seen are well developed, perforating
<i>Solenodon</i> sp.	post. thoracics, lumbar, sacral 1	moderate, few perforating
<i>Desmana moschata</i>	thoracic 9 to lumbar 7	well developed in upper lumbar, perforating ^b
<i>Amblysomus longiceps</i>	thoracic 17 to lumbar 3	moderate, few perforating
Ambiguous:		
Artiodactyla		
?all bovids (cf. <i>Bos taurus</i> , <i>Tragelaphus oryx</i> , <i>Kobus ellipsiprymnus</i> , <i>Boselaphus tragocamelus</i> , <i>Connochaetes taurinus</i>)	post. thoracics and lumbar, but incidence highly variable	tiny, nonperforating, almost always asymmetrical
Tubulidentata		
<i>Orycteropus afer</i>	post. lumbar and sacral 1	Tiny, nonperforating, usually symmetrical
Absent:		
Monotremata: <i>Tachyglossus aculeatus</i> , <i>Ornithorynchus anatinus</i> ; Marsupialia: <i>Didelphis marsupialis</i> , <i>Thylagale billardieri</i> , <i>Vombatus ursinus</i> ; Lipotyphla (other than those listed above): <i>Erinaceus europaeus</i> , <i>Crocodyra attenuata</i> , <i>Microgale talazaci</i> , <i>Hemicentetes semispinosus</i> , <i>Setifer setosus</i> , <i>Potamogale velox</i> ; Xenarthra: <i>Myrmecophaga tridactyla</i> , <i>Bradypus variegatus</i> , <i>Dasyprocta novemcinctus</i> , <i>Priodontes maximus</i> ; Pholidota: <i>Manis gigantea</i> , <i>Manis crassicaudata</i> ; Rodentia: <i>Hypogeomys antimena</i> , <i>Dinomys branickii</i> ; Primates: <i>Loris tardigradus</i> , <i>Lemur catta</i> , <i>Galago alleni</i> , <i>Macaca nemestrina</i> ; Hyracoidea: <i>Dendrohyrax dorsalis</i> ; Perissodactyla: <i>Equus</i> sp., <i>Ceratotherium simum</i> , <i>Tapirus bairdii</i> ; Artiodactyla ^c : <i>Camelus dromedarius</i> , <i>Giraffa camelopardis</i> , <i>Okapia johnstoni</i> , <i>Potamochoerus porcus</i> , <i>Hippopotamus amphibius</i> ; Proboscidea: <i>Loxodonta africana</i> ; Pinnipedia: <i>Phoca vitulina</i> ; Carnivora: <i>Mustela putorius</i> , <i>Lycaon pictus</i> ; *Condylarthra: <i>Phenacodus</i> sp., <i>Meniscotherium terraerubrae</i> ; Pantodonta: <i>Pantolambda bathmodon</i>		

^a In most instances, only one specimen per species examined.

^b Since completing the manuscript for this paper, I have found transarcual canals in posterior thoracic and lumbar vertebrae of *Talpa micura*, *Scalopus aquaticus*, *Parascalopus breweri*, *Scapanus latimanus*, and *Neurotrichus gibbsii*. In these moles (and in *Desmana*) the foramina are laterally displaced onto the pedicles/transverse processes, and therefore are not in the same position as in *Plesiorycteropus*. However, in the absence of any known alternative function for these foramina, I provisionally conclude that the mole condition is ultimately homologous with the one expressed by *Plesiorycteropus*.

^c The "accessory opening" of the transpedicular foramen of *Loris* is not interpreted as a homolog of the transarcual canal (see Vertebral Column, Vascular Features).

^d In the middle thoracics of *Camelus dromedarius* and lumbar of *Giraffa camelopardis* there are small holes, usually nonperforating, on the anterior surface of the neural arch, but displaced toward the transverse processes. In *Okapia johnstoni* the holes are much larger but similarly displaced. In *Potamochoerus porcus* there are well-developed transpedicular foramina, but no transarcuals.

chlorid *Amblysomus*. Here it should be noted that large, symmetrical perforations occur in a number of moles (table 10, footnote b), but in the taxa examined the apertures are po-

sitioned more laterally, outside the apparent confines of the vertebral canal.

The only other taxa which appear to show at least some expression of transarcual canals

are *Orycteropus afer* and bovid artiodactyls (table 10). I emphasize that the canals in these taxa are so small that they are barely distinguishable from randomly occurring nutrient foramina. Because of the relevance of *Orycteropus* to this study, I investigated a number of aardvark skeletons (AMNHM 89008, 90073, 51370, 51909, 51910, and 70189). In all specimens, tiny perforations (sometimes multiple) were found in the same position as transarcual canals in bibymalagasy (fig. 22). None of them was obviously perforating, and few individual vertebrae had perforations on both rims. Perforations were mostly found between Th11 and Lu6, with their greatest expression being limited to the anterior/middle lumbar region. I was not able to determine whether canals are present in *O. gaudryi* because all of the prepared vertebrae in the AMNHP collection were utilized in producing the mounted specimen (AMNHP 22762). The bovid sample showed about the same level of expression as did the aardvarks (i.e., canals tiny, nonperforating, and limited to anterior or posterior sides). As table 10 demonstrates, there is no sign of transarcual canals in erinaceomorphs, perissodactyls, or nonbovid artiodactyls. Canals are also missing in extant hyraxes and the few extinct primitive ungulates available for study. Canals are absent in extant manids and xenarthrans, although tardigradans have other apertures that are worthy of comment (see below).

Given that the transarcual canals of *Plesiorhycteropus* transmitted veins, their homologies and probable function remain to be considered. Although it would be logical to assume that the cardinal system of veins is the ultimate source of the transarcual vasculature, all components of the embryonic postcardinals and supracardinals have been thoroughly accounted for as commonly occurring ontogenetic or pathologic variants in *Homo* and *Felis* (e.g., McClure and Butler, 1925). In any event, these major channels and their dependencies never become incorporated within the vertebral canal. This homology can be decisively rejected.

A better possibility is that transarcual veins are derived from longitudinal venous sinuses within the vertebral canal (the "internal vertebral venous system" of Barnett et al., 1958;

see also fig. 23). These sinuses consist of long axial channels that connect with related internal plexuses that run from foramen magnum to the end of the tail. Two groups of paired longitudinal sinuses are discriminated, the ventral (anterior) and the dorsal (posterior). The ventral sinuses are always the better developed in the few mammals that have been investigated; in some and perhaps most mammals the dorsal pair of sinuses is not developed (Barnett et al., 1958; Reinhard et al., 1962). The ventral sinuses and internal plexus receive spinal veins from the spinal cord, veins linked to the basivertebral veins in vertebral corpora, and, via intervertebral foramina, numerous small veins that help drain body wall tissues, as well as other tributaries. However, as their name indicates they are always situated ventral to the spinal cord, and therefore appear to be unlikely candidates for vessels positioned as in *Plesiorhycteropus*.

In *Homo* there is also a system of small longitudinal sinuses related to the posterior (dorsal) internal plexus. In diagrammatic representations (fig. 23) they are often depicted as single channels, but their structure in humans is better described as retial or plexiform (Reinhard et al., 1962). They receive blood from the spinal veins surrounding the spinal cord, and freely anastomose with the anterior (ventral) internal plexus. They have the correct relations for transarcual veins, although I know of no recorded anomalies in *Homo* that involve the creation of osseous channels in neural arches. Nevertheless, in view of the few facts available, derivation of the vasculature of the transarcual canals from the homologs of dorsal longitudinal sinuses makes the most sense.

The physiological significance of the vascular modifications suggested by the pattern of grooves and canals in bibymalagasy vertebrae can only be surmised. The only living land mammals in which a plausibly analogous system of specializations is known to occur are the tardigradans *Choloepus* and *Bradypus*. In these sloths, part of the systemic return from the caudal part of the body is shunted through the "great vertebral vein," a major vessel that occupies the vertebral canal between the cranial end of the sacrum and the midthoracic region. Morphological

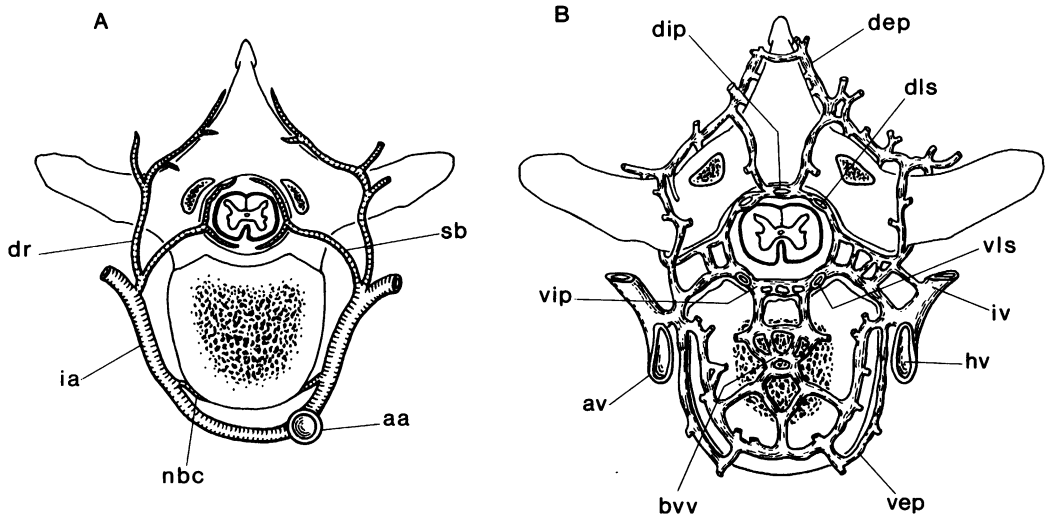


Fig. 23. Vascular network of idealized human midaxial vertebra (after Lessertisseur and Saban [1967b: fig. 386]). A, Arterial network: aa, abdominal aorta; ia, intersegmental artery [intercostal or lumbar]; dr, dorsal ramus of intersegmental artery; nbc, nutrient branch to centrum; sb, spinal branch [or radicular artery]. B, Venous network: av, azygos vein; bv, basivertebral v.; dep, dorsal [posterior] external plexus; dip, dorsal [posterior] internal plexus; dls, dorsal [posterior] longitudinal sinus; hv, hemiazygos v.; iv, intersegmental v. [intercostal or lumbar]; vep, ventral [anterior] external plexus; vip, ventral [anterior] internal plexus; vls, ventral [anterior] longitudinal sinus.

aspects of this system in extant and extinct sloths have been described by Hochstetter (1898), De Burlet (1922), Wislocki (1928), and Hoffstetter (1959), although not all of the channels or mechanisms involved in the shunt have been adequately described. According to these sources, extant sloths (like other xenarthrans) retain throughout life two functional venae cavae which arise from venous plexuses around each iliac artery. In tardigradans, however, only a portion of the venous return is transported back to the heart by the venae cavae; most of it is instead diverted into two or more large trunks that also arise from the iliac plexuses. These trunks, evidently homologous with basivertebral veins, perforate lower lumbar vertebral centra and enter the vertebral canal. Inside the vertebral canal, together with branches of intersegmental veins, they join the great vertebral vein, which appears to be a hypertrophied derivative of one of the anterior longitudinal sinuses (cf. Hochstetter, 1898). At least in embryos and newborn (De Burlet, 1922; Wislocki, 1928), the diameter of this vein is greater than that of the spinal cord. Blood entering the great

vertebral vein is then carried up to the mid-thoracic region, where it drains into enlarged right anterior intercostals (four intercostals in *Choloepus*, only one in *Bradypus*). The anterior intercostal flow is passed into the (proximal) azygos vein, where it continues into the superior vena cava in the usual manner. It should be noted that the rest of the azygos vein, usually responsible for draining the thoracolumbar body wall, is not represented in sloths, presumably because the shunt pirates its area of drainage. Features connected with the tardigradan form of the shunt are said to be missing in armadillos, glyptodonts, and vermilinguans (Hoffstetter, 1959), although so far as I know no soft-tissue investigations have been made to establish whether less (or differently) organized versions of the shunt exist in other xenarthrans. It may be noted here that basivertebral foramina are not at all uncommon among non-tardigradan mammals (e.g., hyraxes), although there appear to be no investigations of their relevant anatomy. Some moles (e.g., *Desmana*) possess both basivertebral foramina in the lumbar and upper sacral regions

and longitudinal foramina on the external aspect of lumbar neural arches (see table 10).

In any case, from a functional standpoint it is not a coincidence, I think, that the largest transarcual canals in *Plesiorhycteropus* are concentrated in the same portion of the spine as the largest basivertebral foramina in sloths and some other mammals. Basivertebral foramina occur in some of the lumbar specimens in the *Plesiorhycteropus* hypodigm, but they are small in comparison to vertebral body size and often asymmetrical (only one off-center foramen). In the sacral fragment (MNHN 1987.043N), however, there is a very large foramen (1.7 mm inside diameter) in the body of Sa2 which opens into the vertebral canal (fig. 19). A similar foramen is found in *Bradypus* (variably in the body of Sa1 or Sa2), in line with the lumbar basivertebral foramina. It is not clear from De Burlet's (1922) descriptions whether or not he detected a similar aperture, but it is not improbable that the basivertebral system of veins extends into the sacral region in at least some tardigradans. In addition, in the bibymalagasy sample the intervertebral foramina formed by middle and lower lumbar are especially large, as are the vascular impressions on their centra. Perhaps venous input in *Plesiorhycteropus* was routed through intersegmental veins, which then linked up with the vessels in the transarcual canals. There are not enough middle and upper thoracic specimens to establish whether or not output could have been sent via hypertrophied right anterior intercostals, although this is the likeliest route for linking up with the superior vena cava.

In the absence of information about soft-tissue structures, we will never know if *Plesiorhycteropus* possessed such a shunt mechanism, although no other explanation for the presence and location of the transarcual canals seems as feasible. A good reason for inferring a shunt is the nature of the vertebral venous system itself. In humans and probably most mammals, the normal maintenance function of the plexiform venous linkages in and around the vertebral column is to drain the spinal cord and related tissues. However, because of rich anastomotic connections with veins in the body wall, brain,

neck, and viscera, it can also serve as a bypass route for venous blood returning from these structures when other routes to the caval system are permanently or temporarily blocked (Batson, 1940, 1957). During sloth evolution, this bypass function was evidently emphasized as a result of, or coordinated with, reduction in the significance of the azygos system. Bibymalagasy may have achieved an analogous result, but by emphasizing different connections.

The marginal transarcual canals of *Orycteropus* and bovids are a different matter. Clearly, they are not involved in venous shunts because they are not organized as longitudinal channels. In these taxa, the transarcual canals—if that is what they are—are involved only in the vascular maintenance of single vertebral elements.

PECTORAL GIRDLE AND FORELIMB

SCAPULA AND CLAVICLE

MNHN 1987.034, a partial scapula from Ampoza, is only tentatively assigned to *Plesiorhycteropus* and will therefore not be extensively compared to members of the comparative set. The specimen (fig. 24; table 11), in poor condition, consists of the glenoid region and the lateral part of the blade. As preserved it exhibits nothing distinctive of tubulidentate, xenarthran, or manid scapular anatomy. The pear-shaped glenoid fossa is basically primitive in aspect. The coracoid process may have been comparatively large, judging from the size of its shorn-off base. There was evidently a superior notch along the cranial border, separating the glenoid portion from the rest of the cranial border of the scapula. This is not evident in figure 24 because the cranial border of the blade is almost entirely missing (possible outline is suggested by dashed line). The caudal border shows some large ridges and deep pits, although it is not possible on the basis of the material preserved to discern whether a "secondary scapular spine" was present. In lateral view (fig. 24, bottom) it may be seen that the profile of the scapular spine curves downward. The acromion, preserved only at its root, also seems to have been caudally directed. Given the elevation of the humeral head above the tuberosities

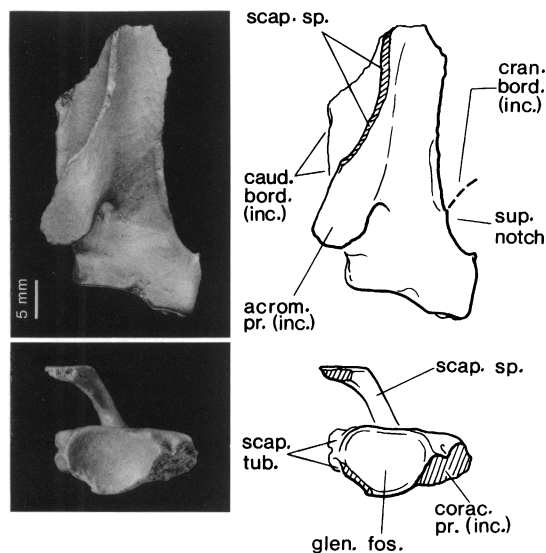


Fig. 24. Scapular fragment, ?*Plesiorhycteropus* MNHNA 1987.034, right side (rev.); **top**, dorsal; **bottom**, lateral views (caudal is toward left). See keys. The suprascapular part of the blade appears deceptively small because most of this part of the blade has been broken off.

(which implies that the arm could be significantly raised in flexion and abduction, fig. 25), it is improbable that the acromion was either large or anterolaterally projecting, as it is in armadillos and aardvarks. However, the fact that an acromion is present at all represents a contrast with hyracoids, which lack this process completely (Fischer, 1986).

None of the features mentioned above conclusively establishes that MNHNA 1987.034 belongs to *Plesiorhycteropus*. However, at present I regard this as highly probable because Malagasy mammals of roughly comparable body mass—medium-sized lemurs, viverrids, and *Tenrec*—seem to be excludable on the basis of morphological differences. In these mammals the scapular spine and the root of the acromion are not downturned: the scapular spine juts out at a right angle, and the acromion tends to rise to a point equal or superior to the dorsal labrum of the glenoid.

A clavicle (MNHNP 1719), 55 mm long, included with *Plesiorhycteropus* specimens in the collection of the Institut de Paléontologie,

is far too large to belong to this taxon; it may be that of a lemur.

HUMERUS

The humerus of *Plesiorhycteropus* is represented by six specimens, most of them damaged (MNHNP 331, 347; MNHNA 1987.031, 035, 036; NHMLP M 7082). Forsyth Major collected NHMLP M 7082 at Antsirabe but for unknown reasons did not describe it. Carleton (1936), who briefly mentioned a bi-bymalagasy tibiofibula from the same locality (see below), must have seen this humerus in the British Museum collection but also failed to mention it. Lamberton (1946) was thus the first to publish a description of the humerus of *Plesiorhycteropus*, employing for the purpose two (?) specimens of unstated provenance.

The humerus of *Plesiorhycteropus* is powerfully built, with a wide distal end, large epicondyles, and well-developed deltopectoral and brachialis crests (fig. 25; table 11). There is no identifiable articular area for the scapular acromion, seen in some armadillos (Hildebrand, 1985). The long axis of the oval, distally elongate head (fig. 25B, E) is set obliquely on the shaft. There are well-marked impressions for the infraspinatus and subscapularis. Good definition of scars for medial and lateral rotators implies that axial rotation was powerful. The deltoid tuberosity is large and laterally projecting, its point of maximum saliency being approximately midway on the shaft. Lateral projection of the deltoid tuberosity maximizes the moment arm of the deltoid for lateral rotation of the humerus, because it moves the line of action of the muscle away from the axis of rotation (Taylor, 1978). The lateral margin of the deep bicipital groove continues distally as a massive crest for attachment of the pectorales, which were presumably large (fig. 25A, D). The prominent, lengthy scar on the medial aspect of the humerus beneath the lesser tuberosity is interpreted as a shared attachment area for the teres major and latissimus dorsi; these two muscles are frequently fused in burrowers, in which they function importantly in digging (Reed, 1951). On the posterior surface (fig. 25B), the proximal limit of the wide area provided for the humeral

TABLE 11
Plesiorhyteropus: Measurements of Pectoral and Forelimb Elements^a

1. Scapula

	SGT	SGV
MNHNA 1987.034	8.2	12.5

SGT, transverse diameter of glenoid

SGV, vertical diameter of glenoid

2. Humerus

	MHL	GTCL	CH	HMD	HAD	AW	BW	CW	TW
MNHNA 1987.031	76.0	74.5	7.9	12.8	15.0	14.0	26.1	7.5	6.5
MNHNA 1987.035	75.1	73.0	7.9	12.8	14.3	13.5	24.5	7.1	6.4
MNHNP 347	—	—	—	11.0	13.4	—	—	—	—
NHMLP M 7082	—	—	7.8	—	—	12.8	20.4	6.4	6.4
MNHNA 1987.036	71.7	70.8	7.9	13.5	13.2	12.0	23.5	7.1	4.9

MHL, maximum length of humerus ($\bar{x}$ = 74.3)

GTCL, distance, proximalmost point on greater tuberosity to distalmost point on capitulum ($\bar{x}$ = 72.8)

CH, height, capitulum ($\bar{x}$ = 7.9)

HMD, mediolateral diameter, head ($\bar{x}$ = 12.5)

HAD, anteroposterior diameter, head ($\bar{x}$ = 14.0)

AW, transverse width, distal articular surface (CW + TW) ($\bar{x}$ = 13.1)

BW, biepicondylar width ($\bar{x}$ = 23.6)

CW, ventral width, capitulum ($\bar{x}$ = 7.0)

TW, ventral width, trochlea ($\bar{x}$ = 6.1)

3. Ulna

	MUL	LOC	LSN	OLA	DCU
MNHNA 1987.039	81.8	26.5	11.0	29.1	76.2
MNHNA 1987.033	—	26.3	10.7	27.2	—

MUL, maximum length of ulna

LOC, length of triceps (olecranon) process, tip to proximal lip of sigmoid notch ($\bar{x}$ = 26.4)

LSN, length of sigmoid notch ($\bar{x}$ = 10.9)

OLA, length, middle of sigmoid notch to proximal end of triceps process ($\bar{x}$ = 28.2)

DCU, length, proximal end of triceps process to distal radioulnar joint

4. Radius

	MRL	MHD	ERL	MTB
MNHNA 1987.032	56.6	9.0	51.4	15.1
USNMP 474081	53.6	8.1	48.9	13.3

MRL, maximum length of radius ($\bar{x}$ = 55.1)

MHD, maximum head diameter ($\bar{x}$ = 8.6)

ERL, length, head to margin of distal articular surface, on medial aspect ($\bar{x}$ = 50.2)

MTB, maximum transverse breadth of distal articular end ($\bar{x}$ = 14.2)

^a Measurements in italics are estimated values (due to breakage); —, not measurable.

origin of triceps is marked by an oblique line, which runs from the margin of the scar for teres major and latissimus dorsi to merge with the lateral supracondylar ridge.

The distal articular surface is transversely small, the distance between the lateral and

medial borders of the trochlea (as measured in distal view) representing only 55% of the biepicondylar width (fig. 25F). The capitular and trochlear portions of the distal articular surface are quite distinct, and there is no non-articular strip intervening between them as

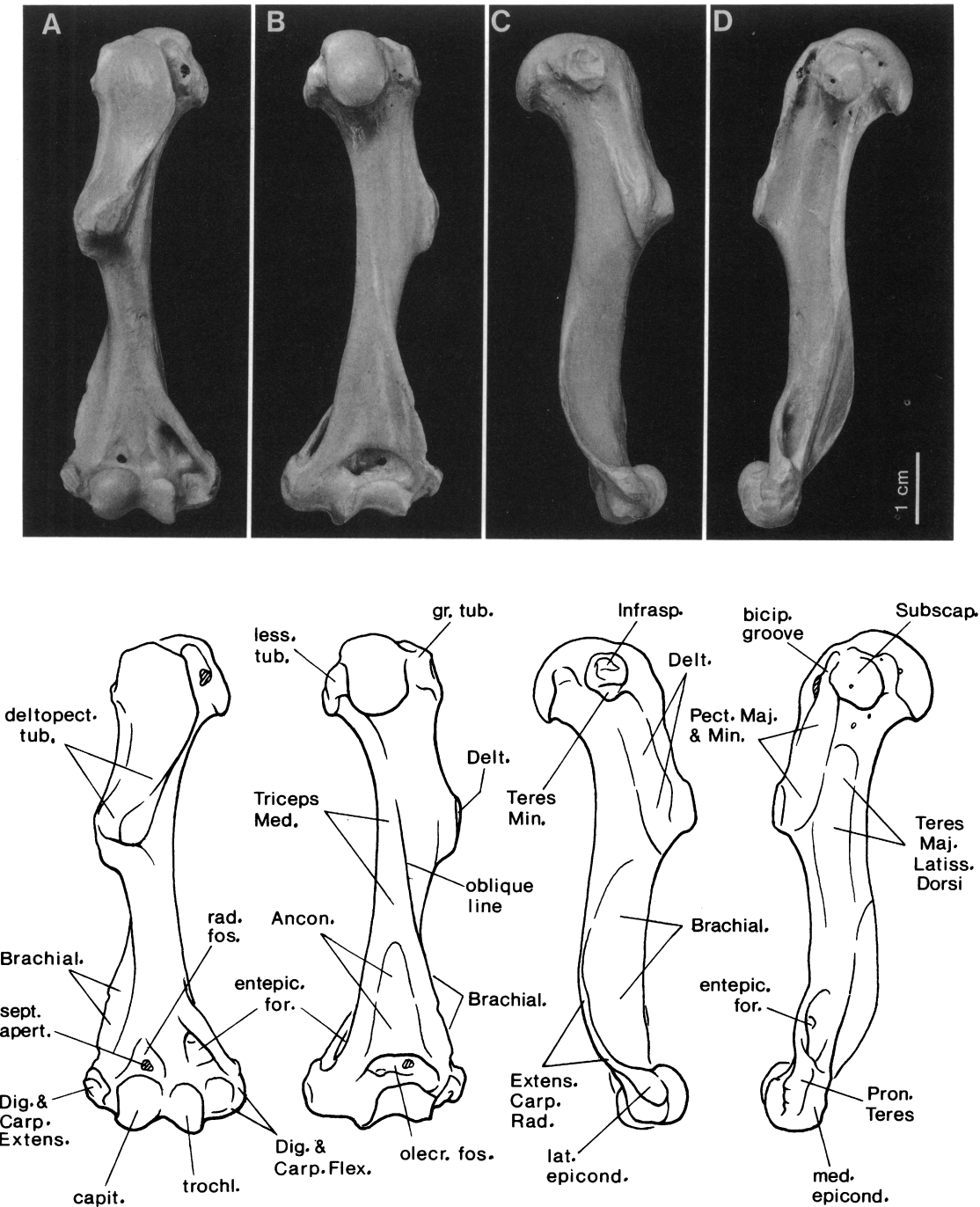


Fig. 25. Humerus, *Plesiorycteropus* sp. MNHNA 1987.036, right side. **A**, anterior (cranial); **B**, posterior (caudal); **C**, lateral; **D**, medial; **E**, proximal; and **F**, distal views. See keys.

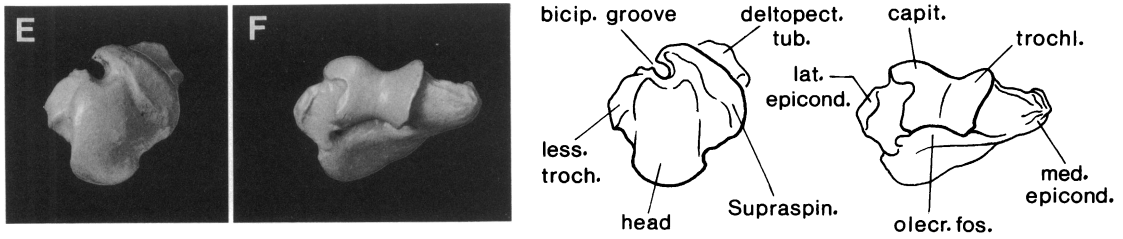


Fig. 25 (continued)

in some fossorial insectivores (Reed, 1951). The articular surface for the radius is restricted to the humeral capitulum per se; there are no accessory continuations of the humero-radial joint surface laterally or medially such as are found in some diggers as a device for strengthening the elbow (cf. Reed, 1951). Lamberton (1946) remarked that the capitulum projects both posteriorly and anteriorly, but it is obvious that it is almost entirely restricted to the anterior (cranial) aspect of the bone (fig. 25F).

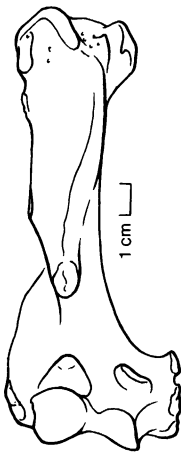
Lamberton (1946) stated that the radial fossa was perforated (i.e., there was a septal aperture or "supracondylar foramen" between the radial and olecranon fossae), but he did not indicate how many of his specimens exhibited this feature. The septal aperture occurs in all examined specimens preserving this area, and on this basis I conclude that perforation is characteristic of bibymalagasy humeri (fig. 25A, B). Whether or not septal apertures are the result of excessive wear by the beak of the olecranon, as might result from habitual extreme extension at the elbow, they occur in a variety of mammals with quite different locomotor behaviors (cf. Lessertisseur and Saban, 1967b). This is pertinent because the morphology of elbow joint surfaces in bibymalagasy indicates that the range of motion in antebrachial extension was quite restricted (see Ulna). Septal perforation does not normally occur in any member of the comparative set, including the semiarboreal moonrat *Echinosorex* (fig. 26). *Plesiorhycteropus* possesses an entepicondylar foramen, a primitive trait widely distributed among extant eutherians.

Most of the traits cited above can be found in a wide variety of mammals, especially diggers, and on the whole they seem to be of

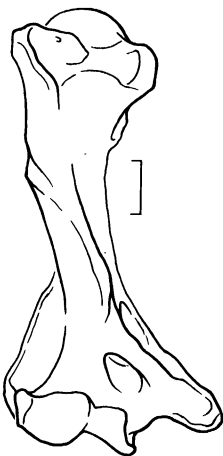
little value for systematic purposes. It is therefore unsurprising that Lamberton's (1946) comparisons to *Edentata did not lead him to any specific conclusions. He noted that *Plesiorhycteropus* and *Dasypus* displayed a few interesting similarities, including the oval, distally elongate head, the shape of the projecting deltoid tuberosity, the form of the shaft, greatly expanded medial epicondyle, and so on. However, these similarities may be contrasted with as many distinctive differences. The humeral head of *Plesiorhycteropus*, although mediolaterally compressed, rises above the proximalmost projection of the greater tuberosity (fig. 25), quite unlike *Dasypus* or *Euphractus* (fig. 26) and implying significant ability to flex and abduct at the shoulder joint (C 20). Compared to armadillos, in *Plesiorhycteropus* the olecranon fossa is much deeper, the lateral epicondyle much more distinct, the lesser tuberosity more projecting, and the deltoid tuberosity less salient.

Lamberton also noted, as another special resemblance between bibymalagasy and armadillos, the great depth and high walls of the bicipital groove. In one specimen from Ampoza (MNHNA 1987.035), not seen by Lamberton, the bicipital groove is converted into a canal by the approximation of the edges of the ridges that face it. In other specimens complete enough for interpretation, the groove is very deep and sharp-edged; it forms about three-quarters of a circle, but is not actually closed over (cf. fig. 25E). Among the members of the comparative set, a complete bicipital canal is seen only in some euphractines (Simpson, 1931; Lessertisseur and Saban, 1967b). The bicipital "tunnel" of some talpids (e.g., *Scapanus*; Reed, 1951) is differently organized and not readily comparable to the bibymalagasy condition. Bicipital ca-

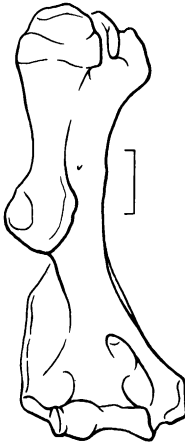
Orycteropus
afer



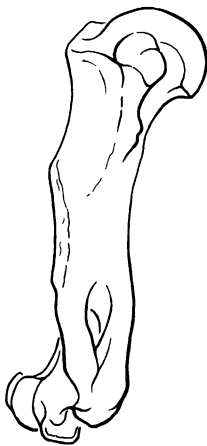
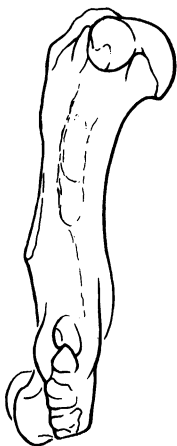
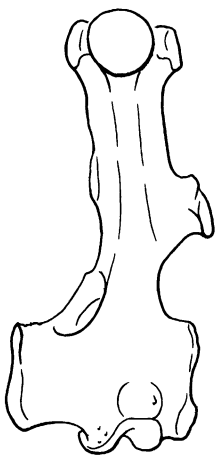
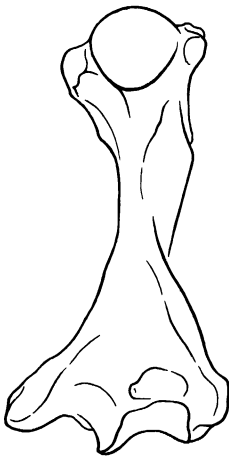
Manis
crassicaudata



Euphractus
sexcinctus



Tamandua
tetradactyla



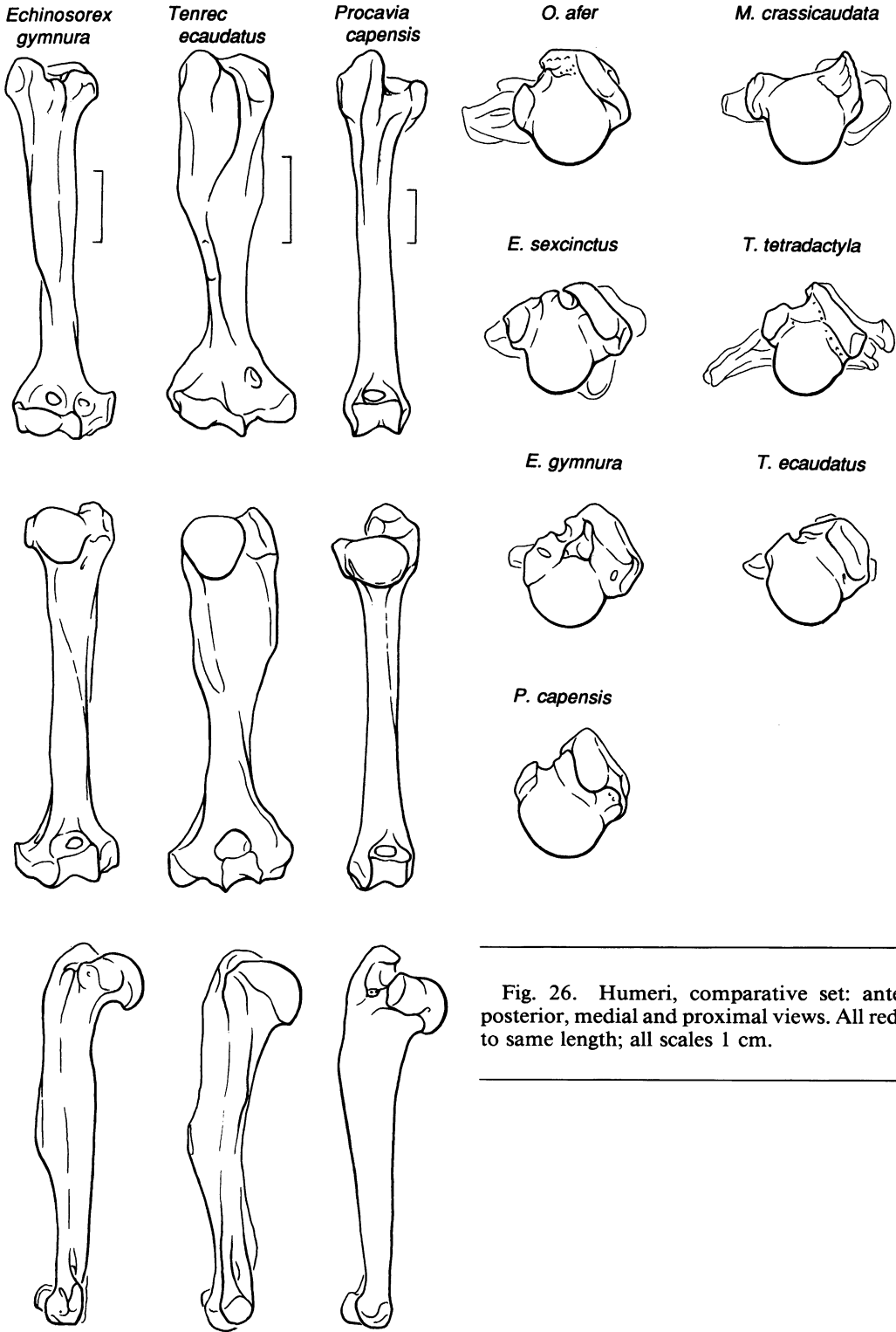


Fig. 26. Humeri, comparative set: anterior, posterior, medial and proximal views. All reduced to same length; all scales 1 cm.

nals also occur in some palaeonodons (Rose et al., 1991).

Lamberton (1946) felt that the humerus of *Plesiorhycteropus* was much more like that of *Orycteropus gaudryi* than *O. afer*, although he did not state precisely what led him to this conclusion. However, his thinking apparently involved a presumed phylogenetic sequence linking *O. gaudryi* to *Palaeorycteropus quercyi*, a supposed tubulidentate known only from a humerus (Filhol, 1894). He made much of the fact that the humerus of *Plesiorhycteropus* is S-shaped in side view, and that this twisting is absent in *Orycteropus* (fig. 26) but present in *Palaeorycteropus*. On the whole, the shafts of all three taxa seem to me to be similarly shaped. The impression of straightness given by the humerus of *Orycteropus* is due chiefly to the lesser development of the deltoid tuberosity and lateral supracondylar line. Other traits that Lamberton cited as resemblances between *Plesiorhycteropus* and *Palaeorycteropus* seem equally indecisive, although it is of some interest that in the Quercy form the humeral head rises above the tuberosities.

Patterson (1975) passed over *Palaeorycteropus* with the comment that it is not orycteropodidlike and should probably be placed in Eutheria incertae sedis. On the whole, he had little to say about humeral morphology, other than to note that the deltopectoral area in *Plesiorhycteropus* is orycteropodid rather than manid in conformation, and that the medial epicondyle is not drawn out into a long, blunt-ended process as it is in manids (fig. 26). He did not mention that *Orycteropus* differed in the form and position of the head (more globular, not obliquely angled, summit not extended above tuberosities), bicipital groove (broadly open, short), deltoid tuberosity (smaller, extends much further down shaft, less laterally projecting), and marked separation of muscular origins on the common flexor epicondyle (fig. 26).

Humeral similarities to manids and myrmecophagids are minor (fig. 26). For its length, the humerus of *Manis* is much more robust and many of its processes and crests are better developed than in *Plesiorhycteropus*. In pangolins (including *Patriomanis*), both tuberosities are powerful and projecting. However,

because they are greatly separated, the pathway for the bicipital groove is a broad, shallow channel rather than a groove. In *Tamandua*, the deltoid tuberosity is much more laterally positioned and distinctly separated from the rugosities for the pectoral musculature, the medial epicondyle much larger, the distal articular surface comparatively more restricted, and the olecranon fossa much shallower. Perhaps the only interesting resemblance, because it has functional implications, is the character of the proximal articular end: in both anteaters and pangolins (including *Patriomanis*, USNMP 299960) the head rises well above the greater tuberosity and is notably rounded at its summit, even more so than in *Plesiorhycteropus* (figs. 25, 26). In extant forms these features are correlated with arboreality (facultative in larger species). Hyraxes (fig. 26) are distinguished by their comparatively enormous greater tuberosity (Fischer, 1986); they differ among themselves (humeral head is more rounded and distal end transversely wider in *Dendrohyrax* than in *Procavia* or *Heterohyrax*), but none shows any important approach to *Plesiorhycteropus* in humeral morphology.

In *Meniscotherium* and *Phenacodus* the humerus is comparatively straight, with large tuberosities that extend above the head (Gazin, 1965). The deltoid eminence is built quite differently from that of *Plesiorhycteropus*, and the bicipital margins are indistinct. The distal end is much narrower transversely.

Hildebrand's (1985) index of biepicondylar width vs. modified humerus length yields a value of 0.35 for MNHNA 1987.031. Among diggers generally this is only a moderate value, although *Dasypus* (0.36), *Zaedyx* (0.39), *Thomomys* (0.35), and *Ctenomys* (0.33), all capable burrowers, are similar.

RADIUS

The bibymalagasy radius, of which three examples are known (MNHNP 333, MNHNA 1987.032, USNMP 474081), is comparatively short and robust (fig. 27; table 11). Before describing the radius, a word about the orientation of this element in the descriptions and figures is needed. As discussed below, joint morphology indicates that the

functional posture of the forearm of *Plesiorhycteropus* was mid-pronation, and its ability to supinate was restricted. Accordingly, the orientation illustrated in figure 27C is approximately equivalent to the true anterior (cranial) aspect, because this is the surface that would have faced rostrally in life. However, the convention is that the sides and borders of the radius should be named according to anatomical position (i.e., full supination)—in which case figure 27A depicts the anatomical anterior aspect. Lamberton (1946) followed conventional orientation in describing the bibymalagasy radius, which helps to explain certain differences between his account and Patterson's (1975). For the sake of clarity, I will follow convention here but will add qualifiers where useful.

The radial head (fig. 27E) is a simple elongate disk, bearing a shallow cup for the humeral capitulum. There are no "extensions" on the lips of the articular surface to increase the size of the radiohumeral joint and lock it against unwanted motion. Such extensions occur in armadillos, manids, and *Orycteropus*, and in lacking them bibymalagasy are presumably primitive.

The proximal radioulnar articular surface, which articulates with the radial notch of the ulna, is very restricted, extending only about 25% around the capitulum (from the 9 to the 12 o'clock positions as seen in fig. 27E). This ulnar facet is separated by a narrow nonarticular band from another facet, situated on the lateral aspect of the head. This second facet cannot have articulated with the radial notch and must therefore be an articular surface for a sesamoid in the extensor mass or the supinator, as in *Manis* (Jouffroy, 1966) and *Tenrec* (personal obs.). Although it is difficult to make out the degree of curvature of the radial head in *Plesiorhycteropus* in the photographs, it is only moderately rounded. This, together with its small size, indicates that axial rotation of the radius was severely restricted (see also MacLeod and Rose, 1993). Experimentation with a radius and ulna whose facets match up tolerably well (MNHNA 1987.032 and 1987.039) indicates that bibymalagasy would have been maximally capable of about 20° of radial axial rotation. This is less than anteaters (50°), and much

less than *Didelphis* (90°), which presumably expresses the primitive condition (cf. Taylor, 1978, 1985). On the other hand, *Plesiorhycteropus* was clearly less restricted in its forearm movements than *Euphractus* and *Priodontes* are. In these armadillos, the proximal radioulnar surface is bevelled flat and is essentially immobile. Hyraxes have a similar radioulnar joint that permits little movement, but Fischer (1986) showed that they are able to achieve a high degree of supination (at the hand) by movements at midcarpal joints.

The radial (bicipital) tuberosity is the slight ridge located immediately below the facet for the radial notch (fig. 27D), essentially in line with the interosseous border. Its small size may correlate with deemphasis of forearm supination suggested by joint surface morphology (cf. Reed, 1951; J. E. Hill, 1937). The radial tuberosity is negligible in hyraxes, armadillos (*Euphractus*, *Dasybus*), and manids (except *Manis gigantea*), in contrast to *Orycteropus* and *Tamandua*, in which it is very pronounced (fig. 28). The narrow neck region is succeeded by the shaft proper, which is moderately bowed and greatly flared. As already noted, because of the position and restricted length of the facet for the radial notch of the ulna, the forearm would have been permanently set in a mid-prone position. In this orientation, the flexor surface (fig. 27A) faces obliquely medially and the extensor surface (fig. 27B) faces posterolaterally. The radius in life position is therefore correctly described as being flattened in the transverse plane, as Patterson (1975) noted. The flexor and extensor surfaces meet along two very prominent borders—the interosseous (fig. 27D) and the oblique (fig. 27C). The flexor surface is dominated in its proximal part by extremely well-defined muscle markings that I interpret as attachments for digital flexors (flexor digitorum superficialis, flexor pollicis longus). The smoother distal part terminates in a blunt projection, in the position of the styloid process of other mammals and identified as such here. The extensor surface is also marked by rugosities for muscle origins (for abductores and extensores of the radial digits). The extensor surface terminates in a major process, which Lamber-

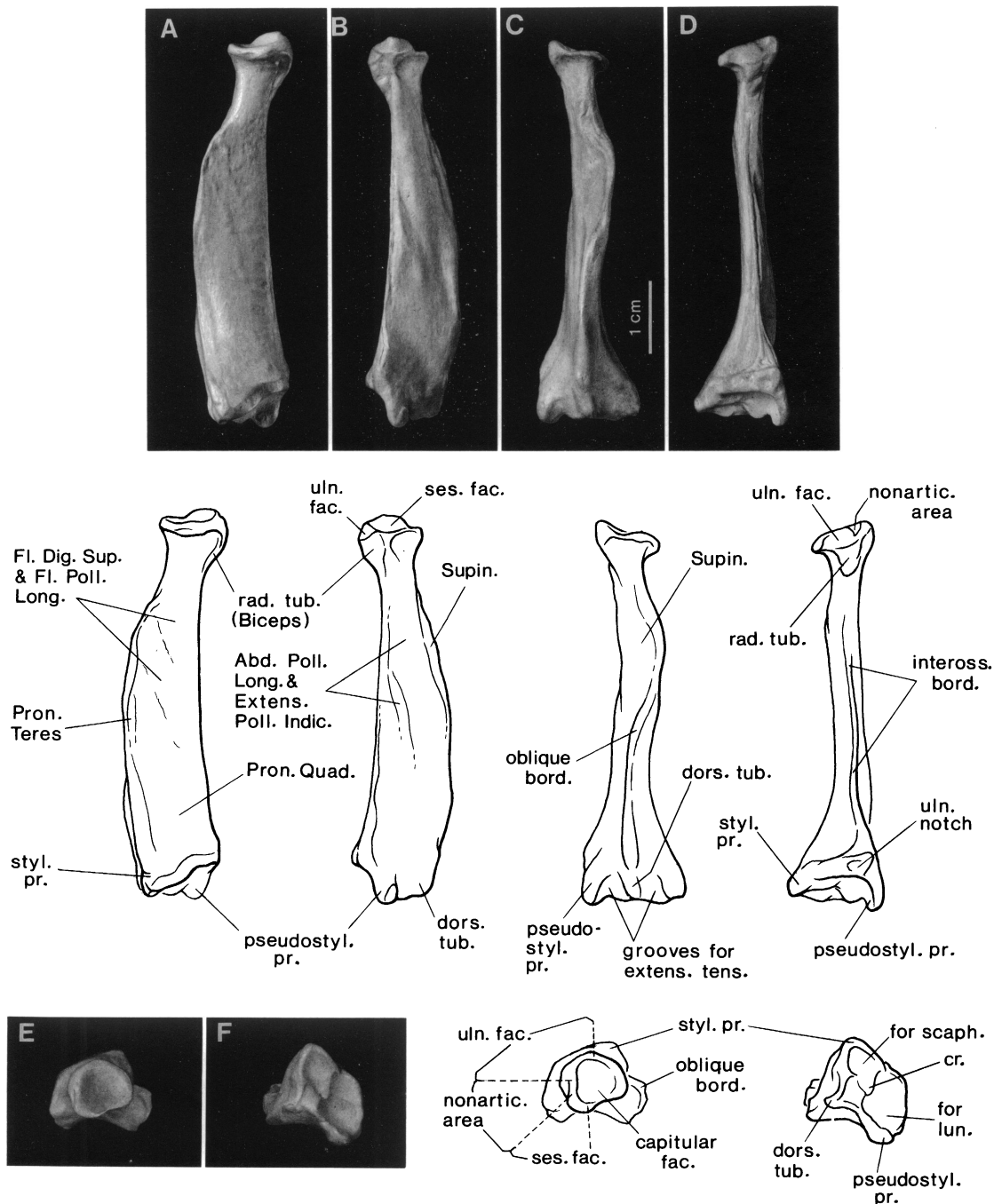


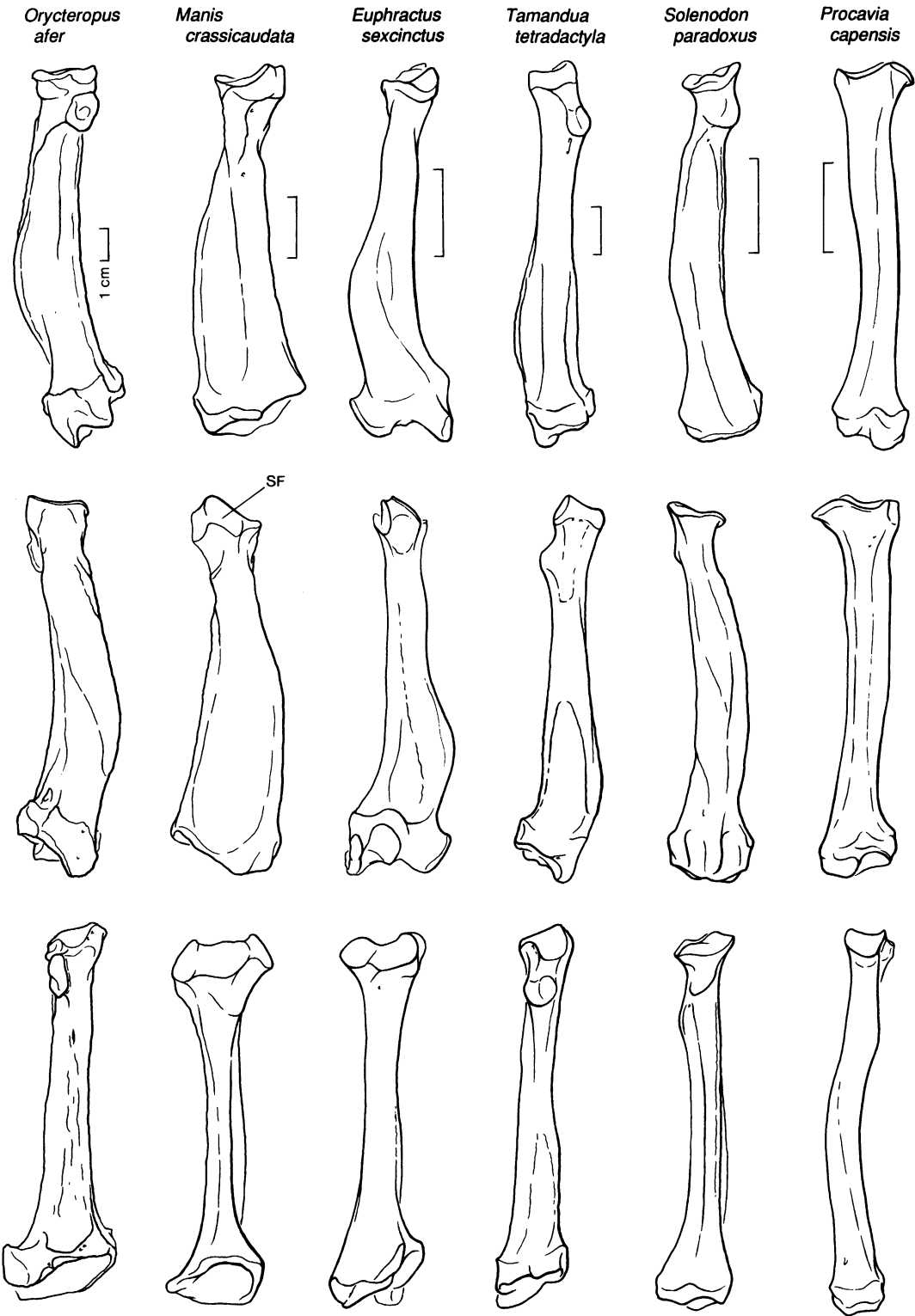
Fig. 27. Radius, *Plesiorycteropus* sp. MNHNA 1987.032, right side. A, anterior (cranial, flexor); B, posterior (caudal, extensor); C, lateral; D, medial; E, proximal; and F, distal views. See keys. Views based on anatomical position, i.e., with radius maximally supinated. In life, radius was probably held in semiprone position and therefore the surface seen in C would face anteriorly.

ton (1946: 39) identified as the "apophyse styloïde." The name is obviously inappropriate, so to avoid confusion I shall refer to it as the pseudostyloid process (cf. similar feature in *Thomomys*; J. E. Hill, 1937). The oblique border is traceable as a sharp, sinuous curve from the neck to the distal end. Distally, this border splits into two daughter ridges, the one running out onto the styloid process, and the other terminating in a large dorsal tubercle on the posterior side of the bone. Among members of the comparative set, the dorsal tubercle is prominent only in armadillos. Like many mammals, including most members of the comparative set, *Plesiorhycteropus* displays deep grooves for extensor tendons on either side of the dorsal tubercle. The interosseous border is straight and sharply defined from the region of the neck to the distal end. The ulnar notch, for the distal end of the ulna, is very shallow and ill defined.

The distal articular end can be partly seen in frontal view and is massively developed. Its profile in lateral aspect (fig. 27C) is comparatively straight except for the pseudostyloid process, which juts farther distally than the true styloid does. In *Orycteropus* there is no pseudostyloid process (fig. 28), and I judge it to be absent in all other members of the comparative set (including *Meniscotherium* and *Phenacodus*). On the distal articular surface itself there are two deeply concave, transversely aligned facets for proximal carpals (fig. 27F). These facets are almost completely separated by a sinuous raised crest and related nonarticular strip. According to their positions, the facet situated beneath the styloid process must be for the scaphoid, and the one located on the other side of the crest must be for the lunate. However, the apparent lunate facet is approximately twice as large as that for the scaphoid—an unusual proportion. Small scaphoids are seen in cursorial mammals that have reduced the number of digital rays on the radial side of the manus (Lessertisseur and Saban, 1967a)—scarcely a likely explanation for reduction in the present case. Armadillos (fig. 28) possess large lunate facets, but their scaphoid facets exhibit interlocking ridges and grooves that are quite unlike the simple concave facet of *Plesiorhycteropus*. Hyracoids (*Dendrohyrax*) and some

lipotyphlans (*Tenrec*, *Desmana*) come closer in scaphoid/lunate proportions, but wrist-joint morphology in these taxa is otherwise quite different. In other extant members of the comparative set, the scaphoid facet is either larger than or equal to the lunate facet. Manid conditions are not directly comparable because the scaphoid and lunate fuse embryonically (Weber, 1928). Among the fossil members of the set, *Meniscotherium* has a lunate facet that is "somewhat larger" than the scaphoid facet according to Gazin (1965: 54, pl. 7), although the contrast between them is not nearly so marked as in *Plesiorhycteropus*. Williamson and Lucas (1992: 17) appear to corroborate this point for *M. chamense*, although they reverse anatomical directions in their description (in anatomical position, the lunate facet is internal).

Lamberton (1946) noted several sharp differences between *Orycteropus* (fig. 28) and *Plesiorhycteropus* in the construction of the radius (shaft tubular rather than flat, bicapital tuberosity well developed, carpal articular surface large but simple). Armadillos and anteaters were scarcely worth comparing to *Plesiorhycteropus*, he stated, but there were some striking similarities to *Manis* (fig. 28), including flattening of the shaft, sharp oblique and interosseous borders, reduction of bicapital eminence, form of the neck, and enlargement of the distal end. (Most of these features are seen in *Patriomanis* USNMP 299960 as well.) For his part, Patterson (1975: 213) allowed that the radius is "the most manid-like bone in the *Plesiorhycteropus* body" but concluded that manidlike traits of the bibymalagasy radius were better "regarded as exaggerations of features present in other orycteropodids." Other features that he identified as being like those of *Orycteropus* were the proportions of the distal articular surface (wider transversely than anteroposteriorly) and subdivision of this surface by a groove. However, a transversely wide distal surface is surely a primitive eutherian feature (cf. presence in *Solenodon*, fig. 28), and mere subdivision of the surface for carpal articulations in *Orycteropus* seems minor in view of the quite different proportions of the lunate and scaphoid facets in *Plesiorhycteropus*. Although the lunate/scaphoid facet proportion is



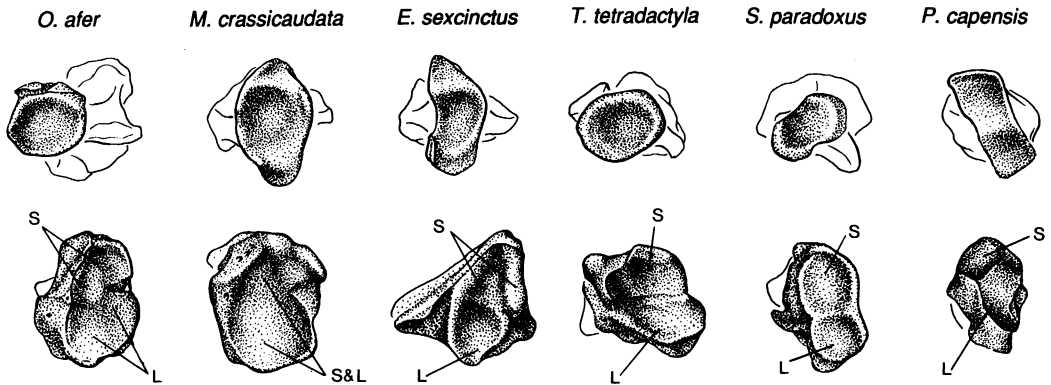


Fig. 28. Radii, comparative set: anterior, posterior, medial, proximal, and distal views. All reduced to same length; all scales 1 cm. L, facet for lunate; S, facet for scaphoid; SF, sesamoid facet.

somewhat similar in *Tenrec*, *Dendrohyrax*, and *Meniscotherium*, very little else about their forearms recalls that of bibymalagasy (shafts not flattened, crests comparatively weak, distal ulna large).

ULNA

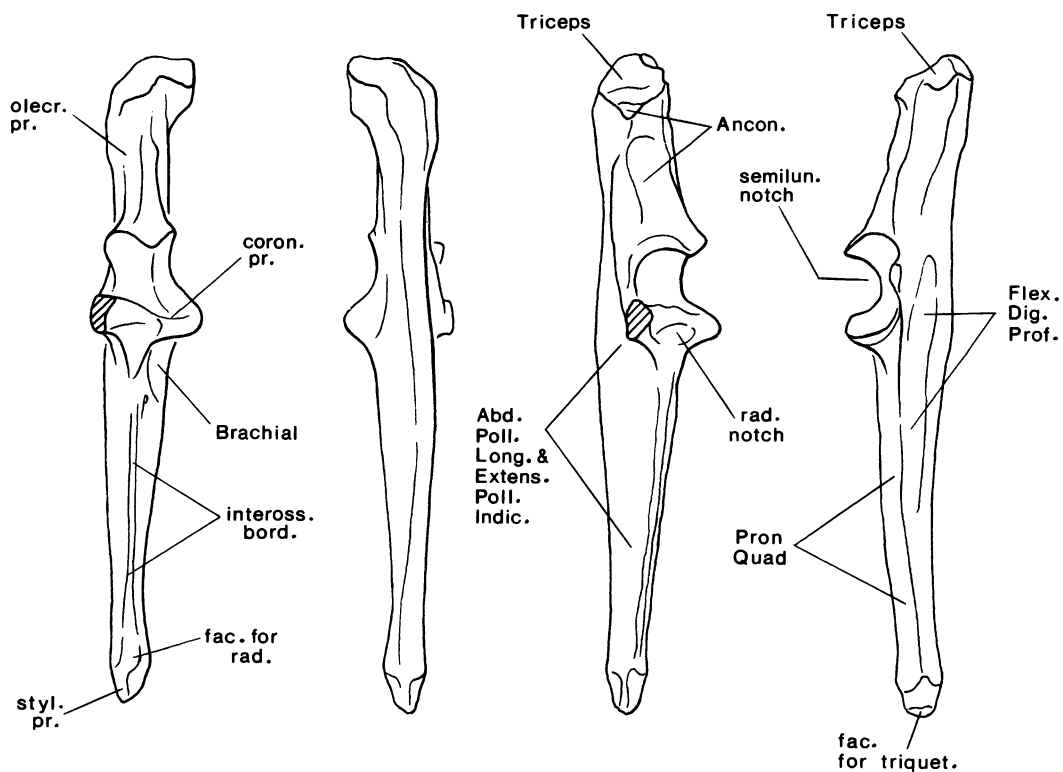
There are three known ulnae of bibymalagasy (MNHNP 330; MNHNA 1987.033, 039). Of these, MNHNA 1987.039, which lacks only a small piece of the radial notch, is the best preserved (fig. 29; table 11). The proximal articulations may be regarded as normal in appearance, but the distal end has only a diminutive, obliquely oriented facet for the triquetral (fig. 29E) and a barely detectable articular surface for the radius.

As Lamberton (1946) noted, the ulna of *Plesiorycteropus* presents two remarkable features: extreme lengthening and proximal widening of the olecranon process, and progressive diminution of the shaft in the distal direction, so that it ends as a spike. In functional terms, the presence of these two attributes in the same ulna can be considered to be almost paradoxical, inasmuch as a greatly elongated olecranon process implies the generation of powerful outforces by the triceps and dorsoepitrochlearis muscles that the diminutive distal end would have been ill equipped to transmit to the carpus. *Plesiorycteropus* surely had some mechanism to transmit force from the ulna to the radius in order to avoid shear at the tiny ulnotriquetral joint

(fig. 29E). The most obvious mechanism—distal radioulnar fusion—not having been adopted in bibymalagasy, force transmission was presumably effected through the interosseous membrane and the great elaboration of ligaments binding the distal radius and ulna together. Since the ulnar and radial shafts were evidently not pressed together as a device to facilitate force transmission (as in burrowing lipotyphlans, rodents, many other examples), perhaps the large pseudostyloid process provided strengthening by acting as an extra area for ligamentous attachments.

Hildebrand's (1985) version of the olecranon index yields 0.53 for the average of two bibymalagasy ulnae (table 13), which is moderately high (approximately equivalent to those for *Manis*, *Zaedyus*, *Orycteropus*, and some moles) but somewhat lower than values he reported for the majority of armadillos, golden moles, and a few others. Thewissen and Badoux (1986) interpret a slightly different index (see table 13) as a measure of elbow extensor mass. Taxa with a large extensor mass always show a high index (*Orycteropus*, 0.35; *Chrysochloris*, 0.39; *Manis gigantea*, 0.30; and *Prionodontes*, 0.40). The value for two bibymalagasy specimens is 0.39. These indices imply that *Plesiorycteropus* produced great force in elbow extension, since the olecranon is the power arm for the elbow extensor mass.

Lamberton (1946: 39) stated that, despite the great size of the olecranon process, the forearm could have been almost fully ex-



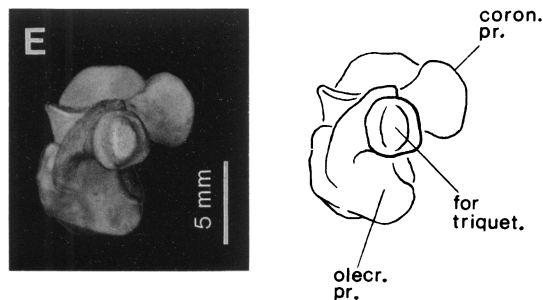


Fig. 29. Ulna, *Plesiorycteropus* sp. MNHNA 1987.039, right side. A, anterior (cranial); B, posterior (caudal); C, lateral, D, medial; and E, distal views. See keys. Distal view with anterior (cranial) surface facing top of page.

tended because of the great depth of the olecranon fossa of the humerus. This seems improbable on the basis of specimens available to me. Among these are a humerus, radius, and ulna (MNHNA 1987.031, 032, 039) that appear to have come from animals of approximately the same size and can be reasonably well articulated to form an arm skeleton. With the elbow joint in approximately full flexion, the ulna can be maximally forced through about 65° of extension on the ulno-humeral articular surface before the beak of the olecranon presses against the floor of the olecranon fossa, terminating motion. Although the frequent and perhaps universal presence of the septal aperture (see Humerus) in *Plesiorycteropus* may be correlated with some locomotor behavior that required maximum extension of the antebrachium, the ability to place arm and forearm in "almost . . . a straight line" (Lamberton, 1946: 39 [trans.]) is clearly out of the question. Restriction of most of the capitular radiohumeral surface to the anterior side of the bone is another indication that the habitual posture of the forelimb was one of semiflexion.

Lamberton (1946: 38) noted that the ulna of *Plesiorycteropus* differs from that of all other edentates except anteaters in having a spikelike distal end. But this observation is not sufficiently emphatic, because even *Tamandua* (fig. 30) does not express the degree of diminution seen in bibymalagasy. The ulnotriquetral joint, only 2 mm in diameter and facing anteromedially, is the only arthroidal

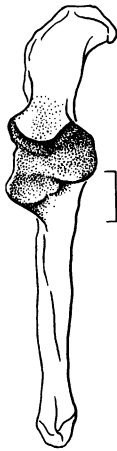
contact between the ulna and the carpus, there being no detectable facet for the pisiform. While it is true that *Orycteropus afer* (fig. 30) also has a comparatively small ulnotriquetral facet, the distal end of the ulnar shaft is not reduced and moreover is marked with a series of pits and ridges for strong liamentous insertions, as is generally the case in other diggers (including the much smaller *O. gaudryi*). In hyraxes (fig. 30) the triquetral facet of the ulna is almost as large in area as the lunate and scaphoid facets of the radius combined. In the condylarthrans *Meniscotherium* and *Phenacodus* (Gazin, 1965) the distal end of the ulna is also broad, even though the carpal facets themselves are not particularly extensive. Considered apart from other evidence, restricted ulnotriquetral contact combined with narrowing of the distal ulna would probably be interpreted by most observers as primitive, as these features are seen in lipotyphlans without highly specialized forelimbs (such as *Solenodon*; fig. 30). In the present case, however, these features are better interpreted as highly derived, because no other digger has an arm organized like that of *Plesiorycteropus*. (*Vombatus* is the extant digger that probably comes closest to bibymalagasy in degree of distal ulnar tapering, but even in wombats the ulnar shaft is robust by comparison.)

In summary, as Lamberton and Patterson noted, and as I have emphasized throughout this section, the forelimb of *Plesiorycteropus* is morphologically distinct from that of any aardvark. The greatest correspondences to orycteropodids occur in features like the shape of the deltoid eminence and the projection of the medial epicondyle, attributes that are nevertheless broadly distributed among diggers. Isolated features can, of course, be selectively chosen to show decided resemblances to armadillos (e.g., depth of bicipital groove, negligible radial tuberosity), manids (e.g., transverse flattening of body of radius), and anteaters (e.g., narrow distal articular surface of ulna). On the whole, however, the phenetic similarities to any single taxon are not so great that a special relationship is indicated. Indeed, it may be just as convincingly argued that *Plesiorycteropus* is comparatively primitive in details of humerus shape, possession of some rotatory ability at the

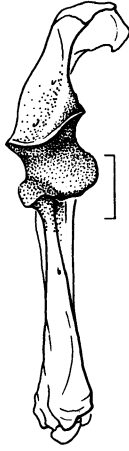
Orycteropus
affer



Manis
crassicaudata



Euphractus
sexcinctus



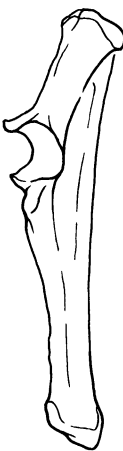
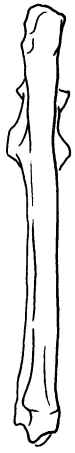
Tamandua
tetradactyla



Solenodon
paradoxus



Procavia
capensis



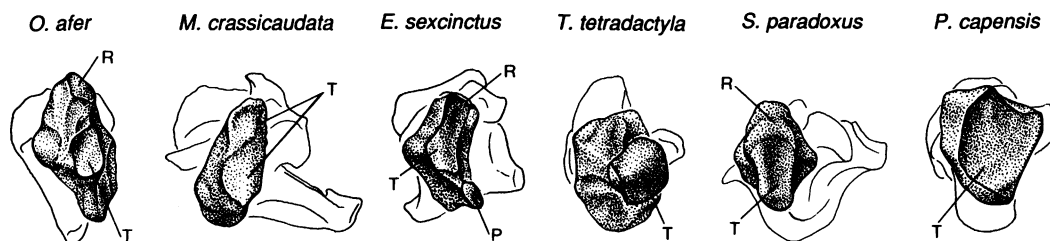


Fig. 30. Ulnae, comparative set: anterior, posterior, medial and distal views. All reduced to same length; all scales 1 cm. Distal views oriented as in figure 29E. P, facet for pisiform; R, facet for radius (distal radioulnar joint); and T, facet for triquetral.

proximal radial joint, separation of scaphoid and lunate, and so on—all of which are seen in *Solenodon* and *Tenrec*. By contrast, the truly remarkable specializations of *Plesiorhycteropus*, such as the extreme reduction of the distal ulna, development of the pseudostyloid process, and possibly the large size of the lunate facet, are not seen in this combination in any other member of the comparative set. Morphology provides some basis for recognizing similar character states (C 21), but distributions do not correspond well with accepted relationships.

PELVIC GIRDLE AND HINDLIMB

INNOMINATE

Lamberton (1946) and Patterson (1975) do not mention the number of specimens that they individually examined, but their descriptions appear to be based mostly on the pelvic girdle (now lost) from *Ambolisatra* (Lamberton, 1946: pl. II). Seven innominates of *Plesiorhycteropus* have been identified in existing collections (MNHN 339, 346, 361; MNHN 1987.030; NHMLP M 7085, unnumbered; PMU M 5095). Most of the currently accessible specimens are highly incomplete, and only one (NHMLP M 7085) preserves both the iliac blade and the pubic symphysis.

Patterson (1975: 215) asserted that the similarity of *Plesiorhycteropus* and *Orycteropus* was at its “most evident in the axial skeleton and pelvis” and that both could be derived from a condylarthran base. Lamberton (1946) was more cautious, stating that with respect to pelvic characters *Plesiorhycteropus* constituted its own “special group” within

**Edentata*. Yet he too concluded that, on the whole, pelvic organization in *bibymalagasy* was more similar to that of *orycteropodids* than any other group to which comparisons could be made. According to these authors, the conformation of the ilium, the position of the acetabulum, and the disposition of prominent muscular attachments such as the iliopectineal eminence were strongly reminiscent of *aardvark* innominates. Patterson noted that *Plesiorhycteropus* differed from *Orycteropus* in the generally “squarish” (as opposed to “trapezoidal”) outline of the pelvis, shorter ischial body, more cranial position of the sacroiliac articulation, and complete absence of the “posterosuperior” (dorsocaudal) extension of the ilium (cf. figs. 31, 32).

It is certainly true that, in terms of the traits discussed by these authors, *Plesiorhycteropus* lacks features distinctive of *xenarthrans* and *pangolins* (cf. fig. 32). However, it is also true that many of the features specially noted by Patterson and Lamberton as *aardvarklike* are in fact more widely distributed among *eutherians* than they acknowledged. Narrow iliac blades with laterally flared margins, relatively long ischial bodies, and prominent muscular attachments are widely distributed among unspecialized quadrupedal *eutherians* (e.g., many rodents and *lipotyphlans*; e.g., *Echinorex*, fig. 32), and caudally directed rod-like pubes and small pubic symphyses are frequently encountered in *diggers* (Hildebrand, 1985). *Meniscotherium*, *Phenacodus*, and *Hyopsodus* have many of these same primitive characters (Gazin, 1965).

The iliac portion of the *bibymalagasy* innominate is prismatic in form, with an elon-

TFDW, mediolateral width of distal end, malleolus to malleolus ($\bar{x}$ = 28.8)

TABLE 12—(Continued)

TFDD, anteroposterior depth of distal end, at right angle to TFDW ($\bar{x}$ = 9.2)
TSW, mediolateral width of tibial shaft at level of cnemial tuberosity ($\bar{x}$ = 5.4)
TSD, anteroposterior depth of tibial shaft, at (and including) cnemial tuberosity ($\bar{x}$ = 14.0)
SSG, distance from center of cnemial tuberosity to intracondylar eminence ($\bar{x}$ = 46.5)
FSW, minimum mediolateral breadth of fibula (taken at transverse level of tibial cnemial tuberosity) ($\bar{x}$ = 2.6)
FSD, anteroposterior breadth of fibula (taken at right angle to FSW) ($\bar{x}$ = 5.9)

4. Astragalus

	PW	MW	ML	TW	TL	NL	HH	HW	MH	EcF	EnF
MNHNP 1655	6.0	17.1	15.3	12.0	8.3	5.5	8.0	7.7	9.2	9.6	4.0
MNHNP 1654	6.1	16.8	15.2	11.8	8.5	5.6	8.5	7.9	11.1	9.5	4.0
MNHNA 1987.044A	6.6	17.4	14.8	11.0	7.7	5.6	8.2	8.2	10.0	9.2	5.0
MNHNA 1987.044B	7.5	16.7	16.6	12.1	8.4	5.6	8.1	7.4	10.4	9.5	5.6

PW, mediolateral width of posteromedial process ($\bar{x}$ = 6.6)
MW, maximum mediolateral width of astragalus (medial aspect of head to fibular facet of trochlea) ($\bar{x}$ = 17.0)
ML, maximum anteroposterior length of astragalus (anterior aspect of head to transverse line intersecting postero-medial process) ($\bar{x}$ = 15.5)
TW, mediolateral width of trochlea ($\bar{x}$ = 11.7)
TL, anteroposterior length of trochlea ($\bar{x}$ = 8.2)
NL, anteroposterior length of head + neck (measured on dorsal aspect, from anterior aspect of head to anterior margin of condyloid facet for medial malleolus of tibia) ($\bar{x}$ = 5.6)
HH, dorsoplantar head height (navicular facet height) ($\bar{x}$ = 8.2)
HW, mediolateral head width (navicular facet only, excluding facet for os tibiale) ($\bar{x}$ = 7.8)
MH, maximum height of astragalus (parallel lines intersecting medial keel of trochlea and plantar aspect of posterome-dial process) ($\bar{x}$ = 10.2)
EcF, ectal facet anteroposterior length ($\bar{x}$ = 9.5)
EnF, ental facet anteroposterior length (actual length of area with articular surface, excluding nonarticular platform that connects articular surface with head) ($\bar{x}$ = 4.7)

5. Metapodials and Phalanges

	ML	HW	BW	SW
MNHNP 1657	30.6	7.2	12.9	6.2
MNHNA 1987.044E	29.3	6.8	—	6.1
MNHNA 1987.044D	27.9	6.7	7.4	5.5
MNHNA 1987.044C	26.5	7.2	7.7	5.5
MNHNA 1987.044F	18.1	5.5	5.0	4.6
MNHNP 1656	19.4	5.7	10.0	5.7
USNMP 474083	17.9	6.7	9.8	5.3
MNHNA 1987.044G	12.8	5.5	7.3	5.5
MNHNA 1987.044H	9.7	5.0	7.0	5.2
MNHNA 1987.044K	16.6	NA	5.2	NA
MNHNA 1987.044J	16.2	NA	6.2	NA
USNMP 474084	15.1	NA	8.8	NA

ML, maximum length (16.9 mm in MNHNP 1656 and 14.0 mm in USNMP 474083 without projecting process)
HW, mediolateral width of head (articular surface only)
BW, maximum width of base (orientation varies; includes projecting process in MNHNP 1656)
SW, midshaft mediolateral width

^a Measurements in italics are estimated values (due to breakage); —, not measurable; ND, not measured; NA, not applicable.

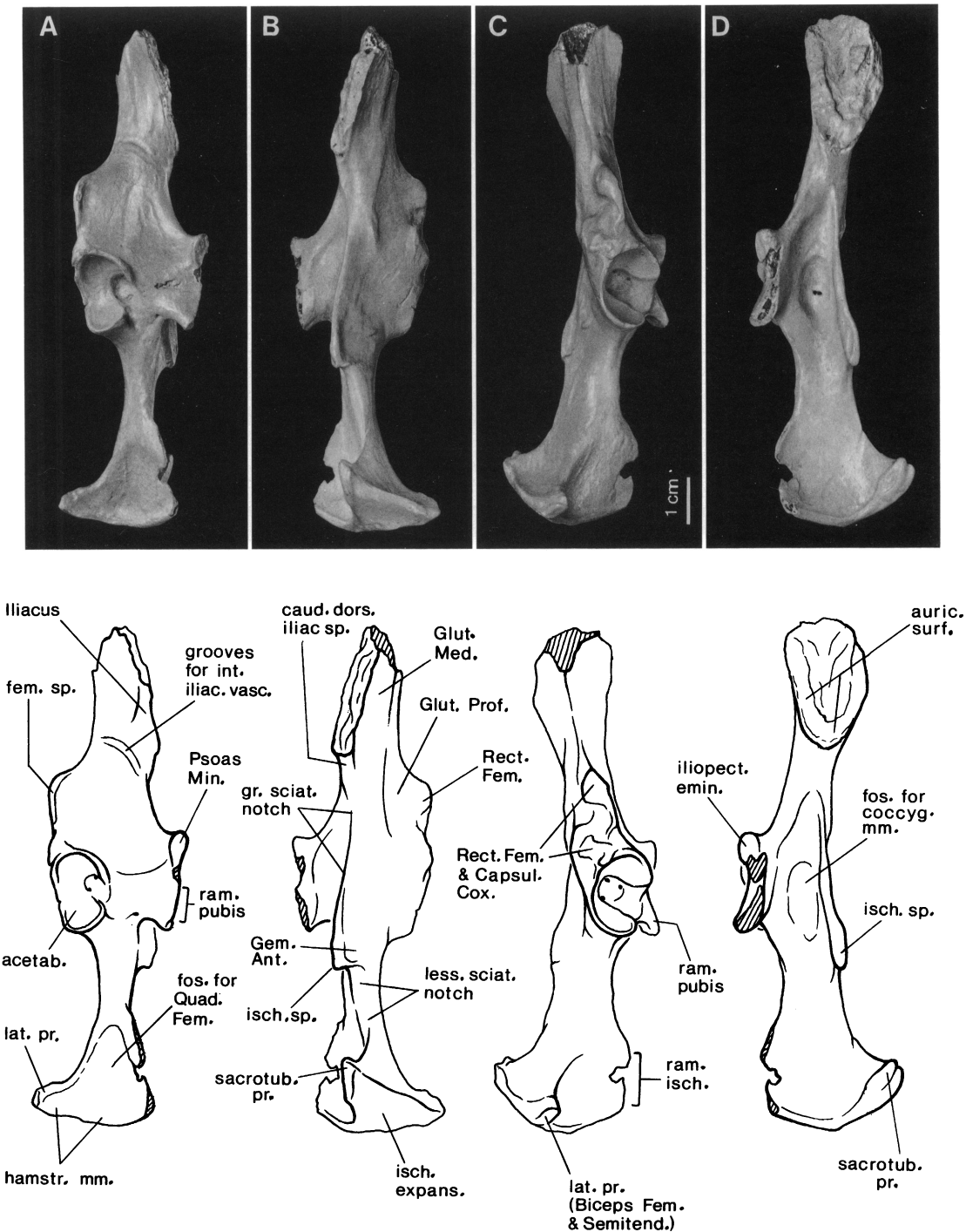


Fig. 31. Innominate, *Plesiorycteropus* sp. MNHNA 1987.030, right side. A, ventral; B, dorsal; C, lateral; D, medial; and E, caudal views. See keys.

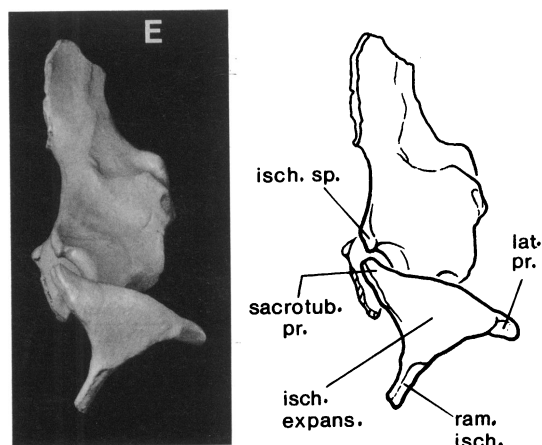


Fig. 31 (continued)

gate body surmounted by a laterally jutting ala (figs. 31, 32). The iliac crest is otherwise without significant dorsal or ventral processes. The gluteal planum is excavated and bears well-marked scars for the limits of attachment of gluteus medius and gluteus profundus. The acetabular margin is surmounted by two massive tubercles equivalent to the femoral spine (fig. 31C). I judge both of these to be for the origin of the rectus femoris (straight head and reflected head), which has a forked or Y-shaped origin in a number of mammals (Jouffroy, 1971a). Alternatively, the more dorsal of the two might represent the place of origin of capsularis coxae. In *Orycteropus*, the femoral spine is large but single (fig. 32). Hyraxes have exceedingly elongate iliac blades with no prominent muscular markings, and are otherwise morphologically quite different (fig. 32).

As noted, *Plesiorhycteropus* completely lacks the dorsocaudal extension of the ilium distinctive of *Orycteropus* (also lacking in condylarthrans). The narrow auricular surface for the sacrum is U-shaped and located well above the transverse level of the acetabulum,

although not nearly so rostrally as in hyraxes. The preacetabular surface, roughly equivalent to the area between the femoral spine and iliopectineal eminence, is larger and more massively built than in *Orycteropus*.

The ischial portion is stoutly built, as may be appreciated by comparing its length to that of the ilium. The total length of the ilium is 86 mm in NHMLP M 7085, the only specimen on which this measurement can be taken (ILH, table 12). MNHNA 1987.030, roughly similar in size to NHMLP M 7085, has an ischium length of 52.0 mm (ISL, table 12). These figures yield a proportional factor of 0.6. In a specimen of *Orycteropus* (AMNHM 51235), the equivalent figures are 149.5 mm (ilium length) and 163.3 mm (ischium length), for a factor of 1.1. In the comparative set (fig. 32), ischia much shorter than ilia appear to be the rule, and thus *Orycteropus* appears to display a derived character state in this instance.

The pubis, intact in only one specimen (NHMLP M 7085), is quite gracile, steeply inclined, and somewhat ventrally prolonged. The pubic symphysis (C 22) is very short. It is probable but not altogether certain that the symphyseal surfaces met; in the reconstruction (fig. 32) no gap is indicated. As can be seen in figure 32, the rami of the pubis and ischium meet at a very acute angle, as in some insectivores (e.g., *Echinorex*) but not *Orycteropus*, in which the ischial ramus angles upward to meet the pubis at a right angle.

The margin of the lesser sciatic notch bears a long, smooth strip, for the bursa of the tendon of obturator internus (fig. 31). This feature indicates that the obturator originated in the typical manner from the sidewalls of the obturator foramen and its membrane. In this respect, *Plesiorhycteropus* contrasts with xenarthrans other than *Cyclopes*, all of which lack a lesser sciatic notch because of extensive sacroischial fusions (C 23).

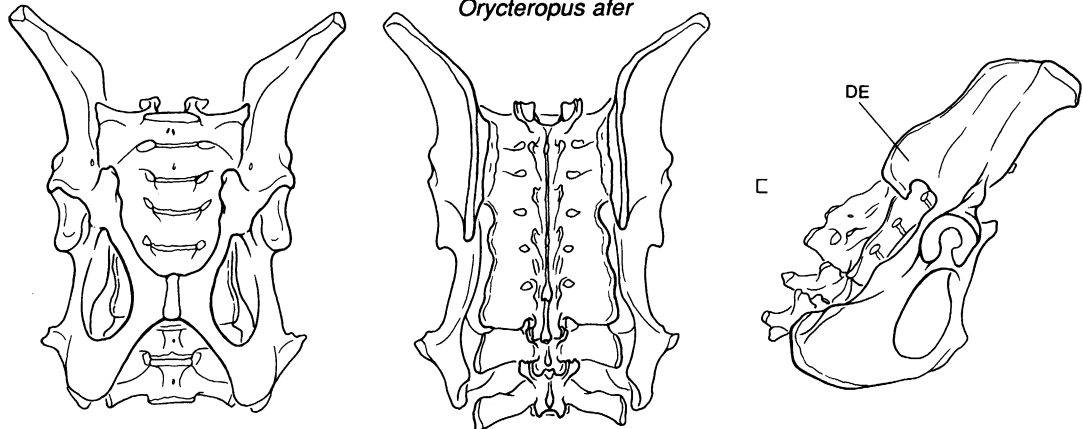
Neither Lamberton (1946) nor Patterson

Fig. 32. Pelvic girdles of *Plesiorhycteropus* and members of comparative set: ventral, dorsal, lateral, and caudal views. All reduced to same length; all scales 1 cm. DE, dorsocaudal extension of ilium, in *Orycteropus*. Representation of *Plesiorhycteropus madagascariensis* is primarily based on Ambolisatra pelvis, as figured by Lamberton (1946: pl. II), with missing parts reconstructed after NHMLP M 7085.

Plesiorycteropus madagascariensis



Orycteropus afer



Manis tetradactyla

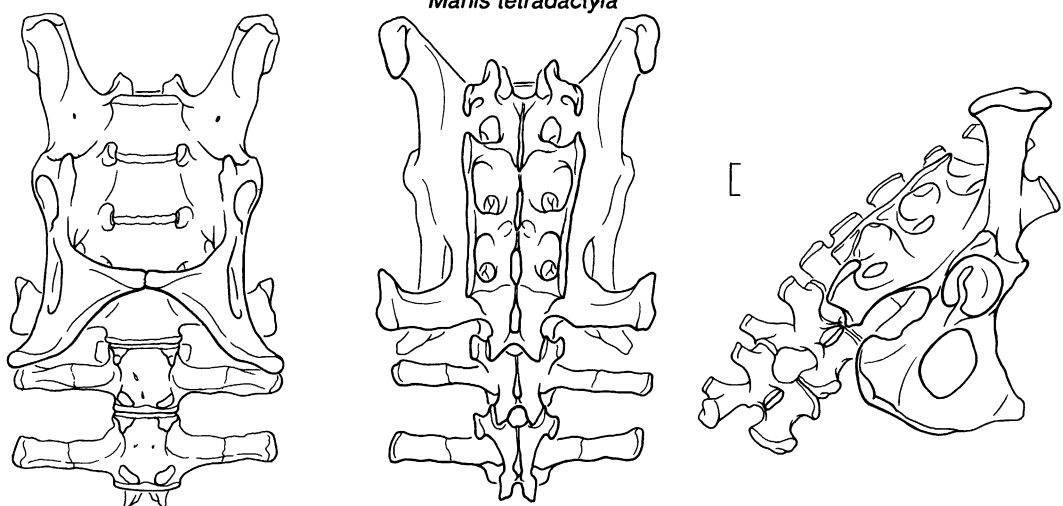
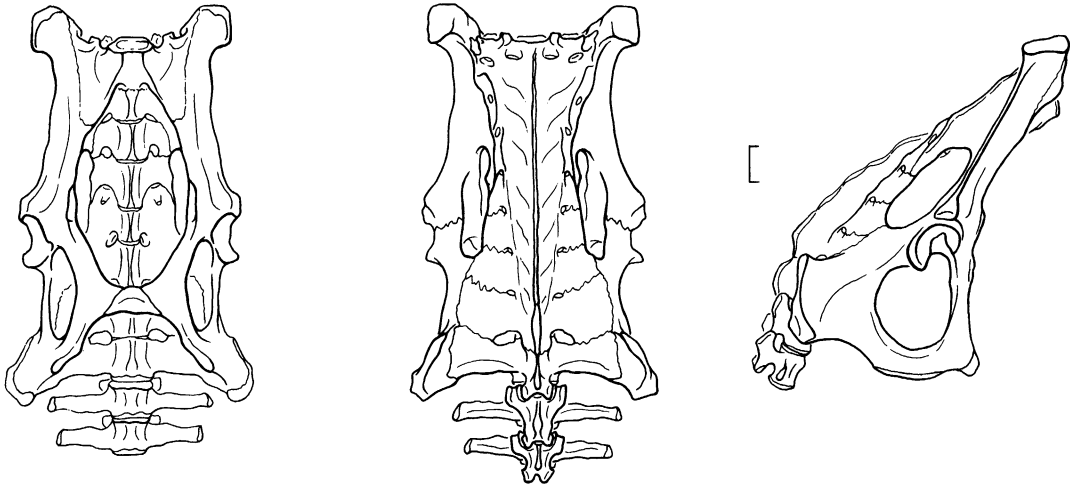
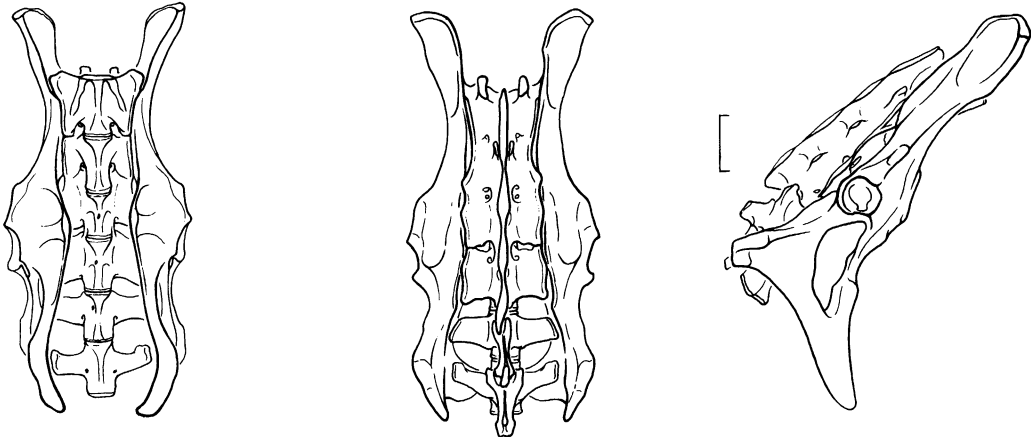


Figure 32

Euphractus sexcinctus



Echinosorex gymnura



Tenrec ecaudatus

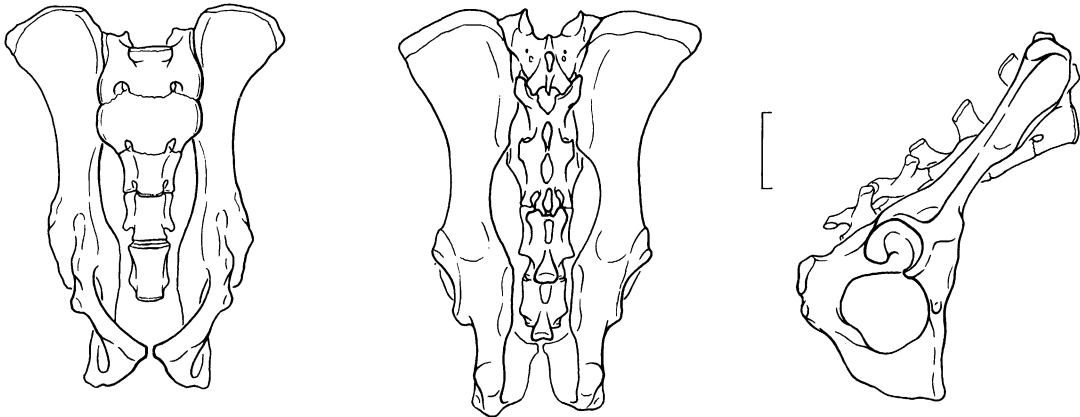


Fig. 32 (continued)

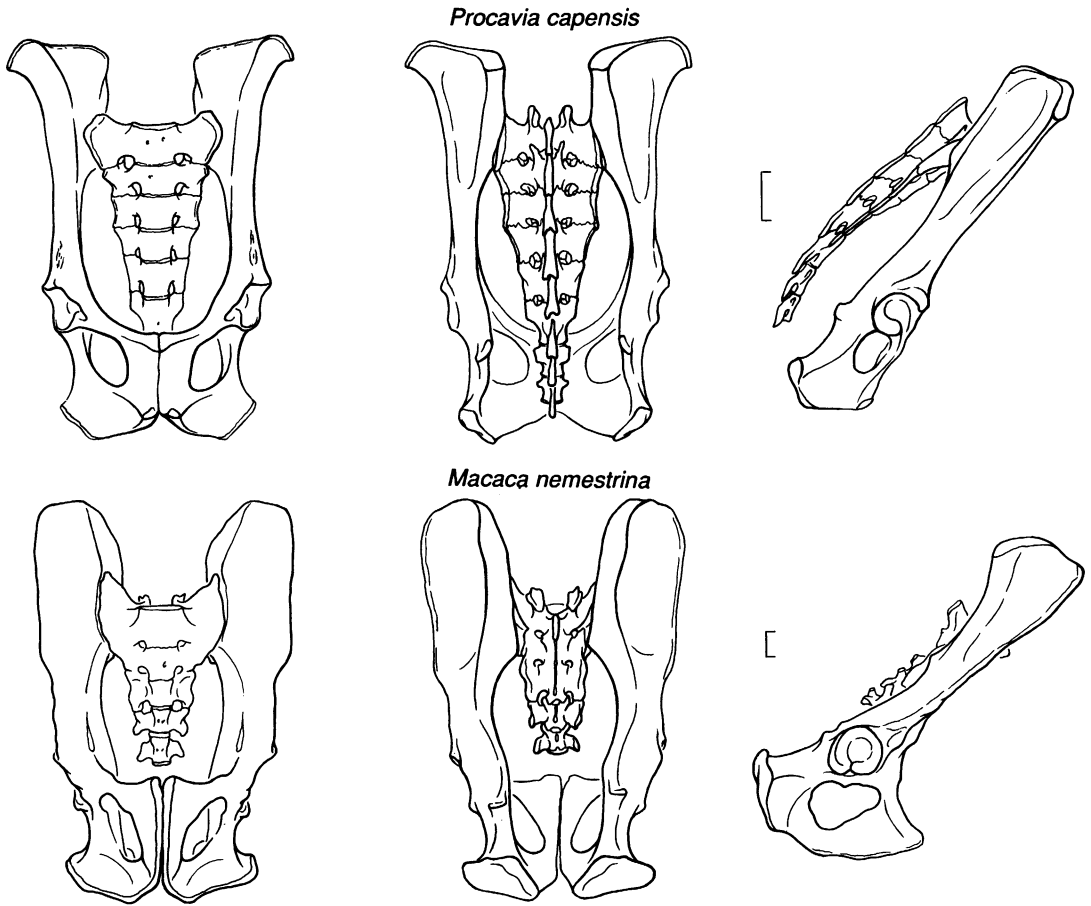


Fig. 32 (continued)

(1975) provided an adequate description of the single most striking feature of the ischium, the modified ischial tuberosity (figs. 31, 32). Primitively, the therian ischial tuberosity is a transversely narrow, rugose pillow of bone; in *bibymalagasy* this area has been transformed into a completely smooth, broad triangular plateau, here termed the *ischial expansion* (C 25). The possible function of the ischial expansion will be considered in a later section (see Function, Adaptation, and Extinction).

Two of the three apices of the ischial expansion are supported by prominent outgrowths that deserve recognition in their own right, here termed the lateral and sacrotuberous processes (figs. 31E, 32). Patterson (1975) regarded the lateral process as the ho-

molog of a similarly projecting but differently positioned outgrowth in *Orycteropus afer*, for which he was unable to ascribe a function (fig. 32; C 24). I find that distinct lateral processes occur in a diversity of other mammals, including wombats (e.g., *Phascolomys*), the caviomorph *Dolichotis*, rabbits, and many ungulates (but not any known condylarthrans). In *Equus*, as in *Orycteropus*, this process is widely separated from the ischial tuberosity, instead of being almost coplanar with it, as in *Plesiorycteropus*. In the horse the process is known as the ventral ischiatic spine, while in *Bos* and lagomorphs it is termed the lateral process or tuberosity of the tuber ischii (Ellenberger and Baum, 1908; Sisson and Grossman, 1938; Craigie, 1948). In these last-mentioned mammals it serves

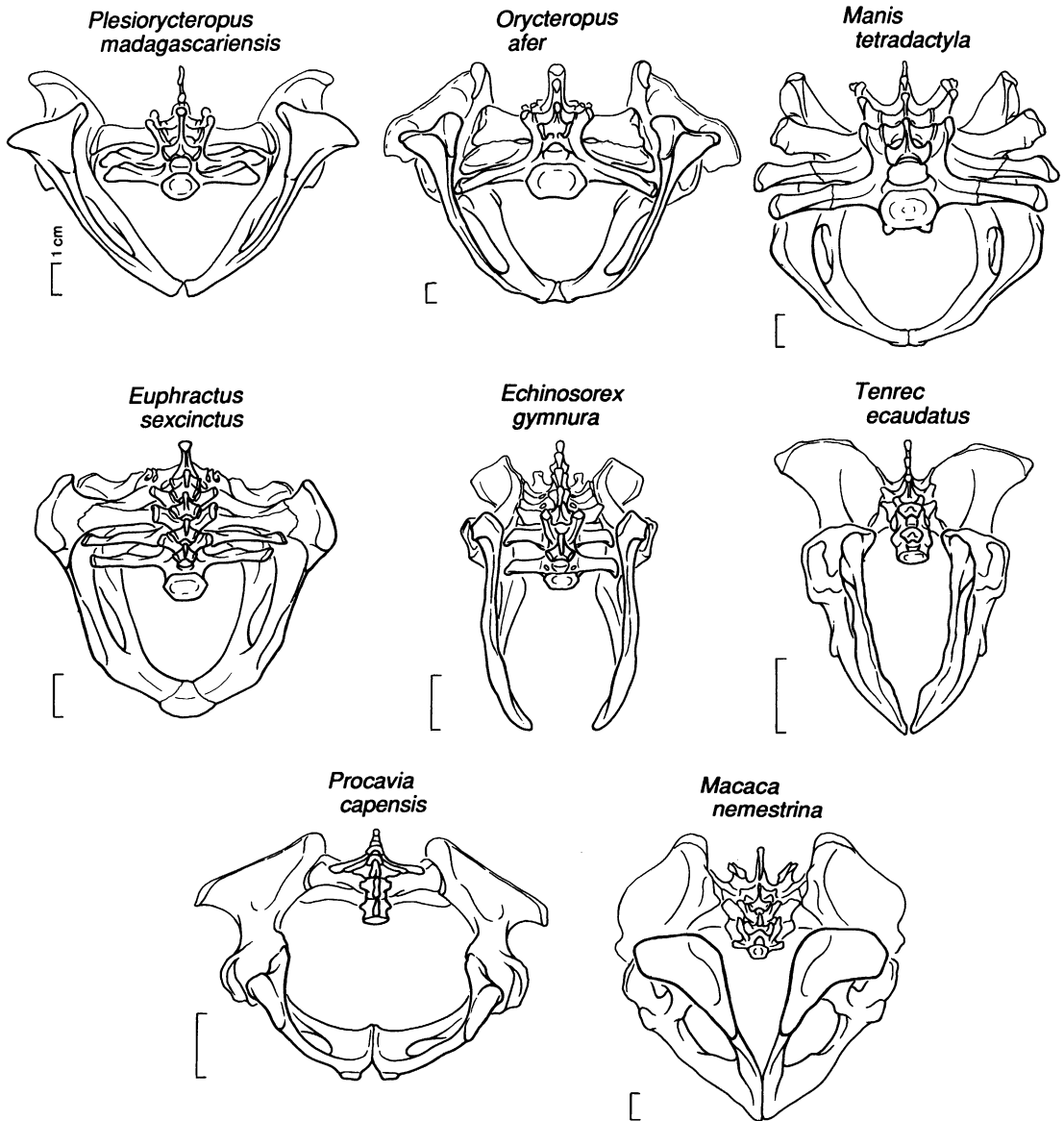


Fig. 32 (continued)

as the point of origin for the biceps femoris (long head) and semitendinosus (deep portion), and I infer that its function is the same in *Plesiorycteropus* and *Orycteropus* (but cf. Humphry [1868], who seems to indicate that it is semimembranosus and semitendinosus that arise from this area in the aardvark).

The ischial expansion's medial process, ambiguously described by Lamberton (1946) and not mentioned at all by Patterson (1975),

is absent in all of the aforementioned taxa, including *Orycteropus afer* and *O. gaudryi*. I judge from the position and orientation of this process that it served as the ischial attachment point of the sacrotuberous ligament, hence "sacrotuberous process". This process helps to form one wall of a deep pocket on the medial aspect of the pelvis, for accommodation of the expanded and conjoined transverse processes of the sixth and seventh

pseudosacrals (cf. fig. 32; Lamberton, 1946: pl. II, fig. B).

A final point of interest is the large fossa, recessed beneath the lateral process, that occupies virtually all of the lateral aspect of the ischial ramus (fig. 31A). In mammals this area normally provides an origin for several muscles (quadratus femoris, hamstrings), and separating out the scars for individual muscles is difficult. However, I suspect that the greater part of this fossa gave rise to an enormously hypertrophied quadratus femoris in bibymalagasy. This is the only muscle that has the correct relations (cf. Jouffroy, 1971a) to insert on the equally large scar on the posterior surface of the lesser trochanter of the femur (see Femur).

FEMUR

The femur (figs. 33, 34; table 12) is the best-represented long bone in existing collections (19 specimens). After demonstrating the unlikelihood of G. Grandidier's (1912) view that this type of femur actually belonged to a giant nesomyine rodent (see Introduction, Synopsis of *Plesiorycteropus* and Statement of Problem), Lamberton (1946) went on to describe the bone in some detail, noting special similarities to femora of dasypodids (cf. fig. 35). Patterson (1975) spent little time on the femur; he allowed that it was structurally quite different from that of *Orycteropus*, but made only cursory comparisons to armadillos, armadillos and manids. He also had little to say about femoral structure in condylarthrans, other than that it was "closely comparable" to that of *Plesiorycteropus*.

The similarity to dasypodid femora is striking only in anterior (cranial) aspect (cf. figs. 33, 35). As in armadillos, the anterior surface of the shaft in bibymalagasy has a projecting, fluted appearance, seeming to expand smoothly from the massive, vertically aligned greater trochanter all the way to the condylar end. Fluting is set off by the flare of the three trochanters. The same distinctive features are seen in condylarthrans, of which *Meniscotherium* is a representative example (cf. Gazin, 1965). By contrast, in *Orycteropus afer* (fig. 35) the anterior diaphyseal surface has no salience, the greater trochanter is lower and differently proportioned, and the lesser

trochanter is barely evident when the bone is viewed from in front. For its size, the femur of *Orycteropus gaudryi* is somewhat more gracile than that of extant *O. afer*, but it agrees with the latter in all essential morphological details. Extant manids (fig. 35) are conspicuously different in exhibiting a flattened rather than barreled shaft and tiny lesser and third trochanters. In addition, the third trochanter is situated just above the level of the lateral condyle (Emry, 1970), clearly a derived condition. *Patriomanis* (USNMP 299960) is much less derived, but its greater and lesser trochanters are quite small by comparison to those of *Plesiorycteropus*. Myrmecophagids, tardigradans, lipotyphlans, and hyraxes (fig. 35) evince no close resemblances to bibymalagasy.

In posterior (caudal) view, *Plesiorycteropus* differs from all dasypodids in the size and degree of projection of the lesser trochanter (cf. figs. 33B, 34B, 35; C 26). *Plesiorycteropus* also possesses a deep trochanteric (digital) fossa; this feature, absent or barely suggested in pangolins and armadillos and other extant xenarthrans, is present in *Orycteropus*, *Echinosorex*, *Dendrohyrax*, and the condylarthrans listed above. Notably absent from *Plesiorycteropus* is the pectineal tubercle or "fourth trochanter" (Howell, 1941), an orycteropodid synapomorphy present in *Orycteropus*, *Leptorycteropus*, and *Myorycteropus* (Le Gros Clark and Sonntag, 1926; MacInnes, 1956; Patterson, 1975). This feature is said to occur inconstantly in some hyracoids (Lessertisseur and Saban, 1967b), but in the comparative set I illustrate the pectineal tubercle for *Orycteropus* only (fig. 35).

Plesiorycteropus is distinguished from all members of the comparative set, with the minor exception of *Echinosorex*, by the length and definition of its femoral neck (cf. figs. 33–35). Indeed, the length of the neck in bibymalagasy seems to match or exceed conditions found in most rodents, primates, and carnivores, three groups for which long femoral necks are typical. Long necks are usually interpreted as facilitating the mobility of the hindlimb (Lessertisseur and Saban, 1967b), but in digging mammals necks are usually inconspicuous and the head is accordingly situated close to the long axis of the femur (cf. Reed, 1951). *Orycteropus* lacks a definite

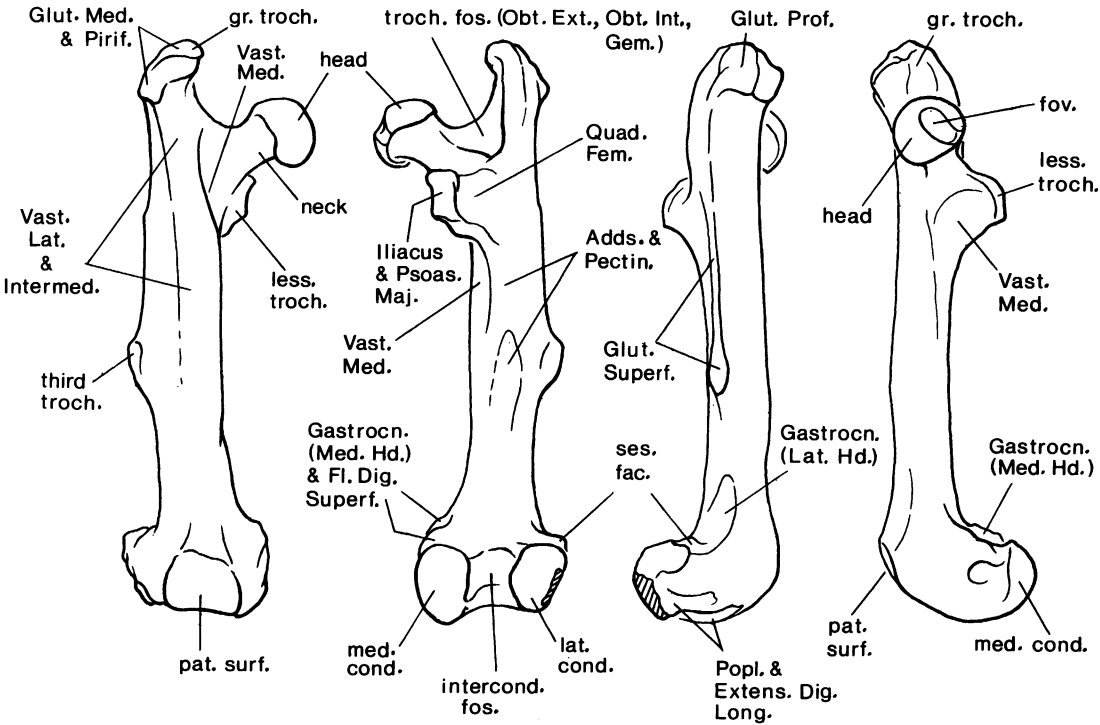


Fig. 33. "Small" femur of *Plesiorycteropus*, attributed to *P. germainepetterae*. A, anterior (cranial); B, posterior (caudal); C, lateral; D, medial; E, proximal; and F, distal views. See keys. A–D, MNHNP 329, apparent right side (reversed to facilitate comparison with fig. 34); E and F, MNHNP 343, apparent right side (reversed), attributed to *P. madagascariensis* but scaled to MNHNP 329.

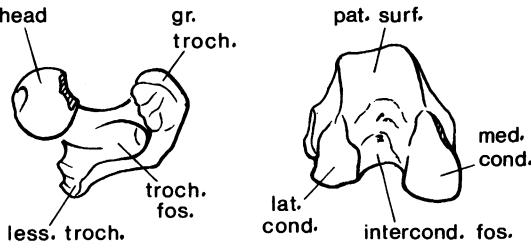
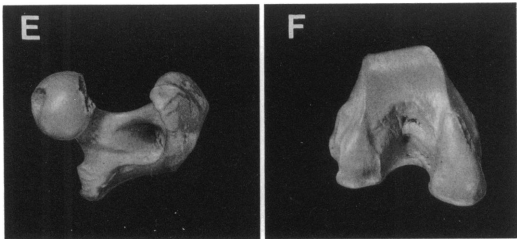


Fig. 33 (continued)

neck, although *Myorycteropus* exhibits a short one (MacInnes, 1956). *Tenrec*, a burrower (Eisenberg and Gould, 1970), has essentially no neck; *Echinosorex*, the only lipotyphlan with confirmed highly arboreal habits, has a very significant one. *Meniscotherium* is intermediate in this regard (Gazin, 1965), as are hyraxes.

Lamberton (1946) described the femoral head as an almost-perfect hemisphere, but failed to note that the large, elongated, ventroposteriorly located fovea almost completely interrupts the head's posterior surface (figs. 33B, 34B). Complete or nearly complete interruption of the articular surface is rare among eutherians (C 27). Absent are the more

radical sorts of head modification seen in some burrowers (Reed, 1951).

When the bibymalagasy femur is positioned vertically on a surface and viewed from the medial side, the neck can be seen to leave the shaft at an angle of approximately 60°. *Dasypus* and *Echinosorex* are comparable, but in *Orycteropus* and *Manis* the neck is more vertically aligned and the angle is therefore closer to 80–85°.

In bibymalagasy the greater trochanter (figs. 33, 34) extends to a very significant degree above the level of the femoral head, in contrast to *Manis*, *Patriomanis*, *Tamandua*, *Bradypus*, *Procyon*, and *Tenrec*, but similar to *Dasypus* (and, to a lesser degree, *Meniscotherium* and *Echinosorex*). Le Gros Clark and Sonntag (1926) stated that the greater trochanter rises above the femoral head in *Orycteropus*, which is true, but only to a trivial extent. On the cranial aspect of the greater trochanter there are pronounced scars and ridges for the insertions of the middle and deep gluteals and the piriformis (cf. 33A, E). Laterally, the trochanter is continuous with the cranial part of the long crest that terminates, more than halfway down the shaft, as the third trochanter (fig. 33C). The crest and third trochanter represent attachment sites for an evidently large and distally extensive superficial gluteal, which suggests good powers of hindlimb abduction and hip flexion. Although many mammals have a small tubercle or ridge at the point of distal insertion of gluteus superficialis, a large crest like that seen in *Plesiorycteropus* is rarer. Crestlike third trochanters are not uncommon, occur-

TABLE 13
Plesiorycteropus: Limb Indices^a

Indices	Measurements	Values
1. Intermembral Index:	(MHL + MRL)/(MFL + MTFL)	0.61
2. Brachial Index:	MRL/MHL	0.74
3. Olecranon Index I: ^b	OLA/(MUL – OLA)	0.53
4. Olecranon Index II: ^c	(LOC + 0.5 LSN)/MUL	0.39
5. Crural Index:	MTFL/MFL	0.79

^a "Values" are computed from averages (where applicable) given in tables 11 and 12; in most cases species allocation is not determinable and is therefore not taken into account here. Acronyms for measurements as in tables 11 and 12.

^b Index as defined by Hildebrand (1985).

^c Index as defined by Thewissen and Badoux (1986).



Fig. 34. "Large" femur of *Plesiorycteropus*, attributed to *P. madagascariensis*, MNHNA 1937.038 (holotype of "*Hypogeomys*" *boulei* [G. Grandidier, 1912]). A, anterior (cranial), and B, posterior (caudal) views. Compare figure 33.

ring in mammals as diverse as insectivores (e.g., *Solenodon*, *Tenrec*), rodents (e.g., *Hypogeomys*, many caviomorphs), *Orycteropus*, perissodactyls, dasypodids, some strepsirhine primates, and many others (e.g., *Patriomanis*).

I interpret the noticeable ridge on the anterior aspect of the femur, spiraling from the base of the greater trochanter over to the medial surface of the shaft, as a line that demarcates the areas of origin for vastus lateralis and intermedialis from that for vastus medialis. Other muscle markings that can be interpreted are indicated on the keys to figure 33.

The lesser trochanter also bears extensive muscle scars. The medial or leading edge of the trochanter (fig. 33B) bears a pronounced rectangular marking, which I interpret as the

insertion for iliacus and psoas major. Quite distinct from the latter is a very extensive, vermiculated scar, apparently for a muscle, that covers all of the posterior surface of the lesser trochanter and extends onto the shaft proper (figs. 33B, 34B). I interpret this feature as the area of insertion of the quadratus femoris (see Innominate). It cannot be for either pectineus or iliopsoas, since there are discrete scars in positions typical for the insertions of these muscles on the medial edge of the trochanter. Because the scar is essentially restricted to the trochanter and the contiguous portion of the shaft, it is extremely unlikely that it relates to insertion of the adductores or biceps femoris. Finally, because there is a deep trochanteric fossa for reception of the obturators and gemelli, the scar cannot represent an insertion for those mus-

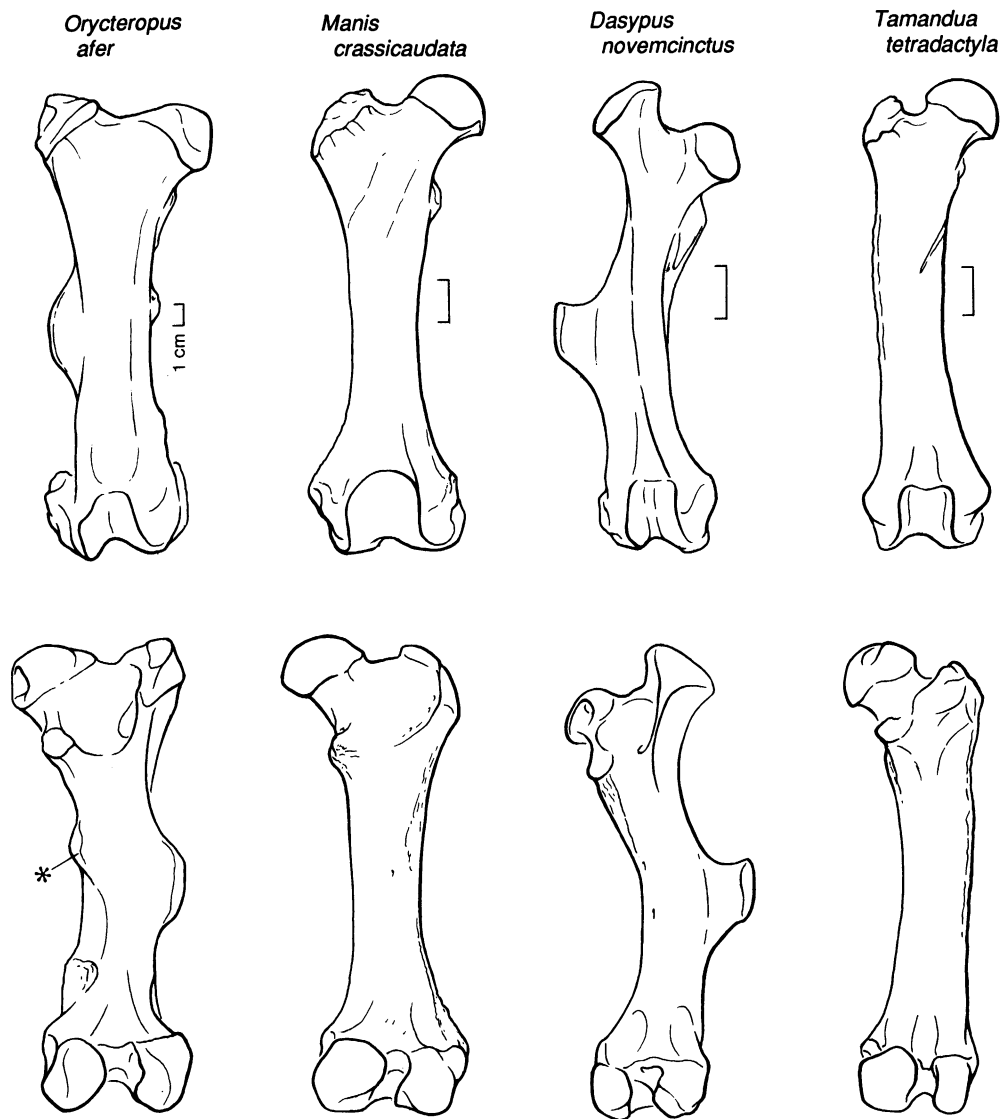


Fig. 35. Femora, comparative set: anterior and posterior views. All reduced to same length; all scales 1 cm. Asterisk, pectineal tubercle ("fourth trochanter").

cles. *Faute de mieux*, this scar is best regarded as the insertion for a vastly hypertrophied quadratus femoris. This is clearly a highly derived feature, and contrasts strongly with the oppositely apomorphic condition alleged for *Orycteropus*, in which this entire muscle is said to be absent (Le Gros Clark and Sonntag, 1926). (Humphry [1868: 312], however, merely stated that quadratus femoris is not a "distinct" muscle in *Orycter-*

opus.) Armadillos are said to possess a large quadratus femoris (Galton, 1870), but I find that an identifiable scar for this muscle is discernible only in *Priodontes*. Muscular scars in this region are negligible in *Manis*, *Tamandua*, and *Bradypus*. A large and flaring lesser trochanter is found in *Meniscotherium*, and as a further similarity to *Plesiorycteropus* there is a slightly raised ridge that extends from the base of the trochanter almost to the

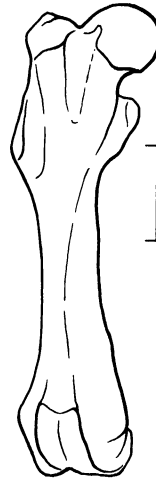
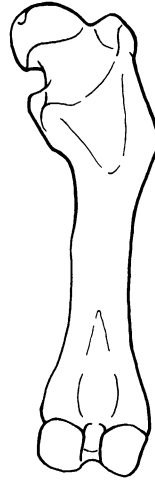
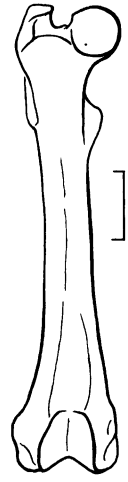
*Bradypus
variegatus**Echinosorex
gymnura**Tenrec
eacaudatus**Procavia
capensis*

Fig. 35 (continued)

lateral border of the femur. Hyraxes must be referenced here because they have large muscle scars in the same location, although Jouffroy (1971b) found nothing remarkable in the size and disposition of quadratus femoris in *Dendrohyrax* (C 26).

As Lamberton (1946) noted, a distinctive feature of the large distal end of the bibymalagasy femur is the great size and shallow depth of the patellar or rotular surface (fig. 33A, F). The patellar surface is moderately to deeply grooved in all members of the com-

parative set (fig. 35) except *Manis* and *Bradypus*. Deep grooving is especially obvious in *Orycteropus* and *Myorycteropus*, somewhat less so in *Echinosorex*, *Tenrec*, and *Meniscotherium*. *Dasypus* and *Euphractus* display a more moderate degree of grooving, with *Priodontes* exhibiting the shallowest patellar surface seen in extant armadillos. Interestingly, grooving is quite well developed in *Patriomanis*, in contrast to extant manids.

A flat patellar surface is found in some extant diggers (e.g., *Scapanus*), but this feature

is not general among fossorial mammals. *Hypogeomys* (and most other rodents, for that matter) exhibit deeply grooved patellar surfaces, which is one more reason for rejecting the argument that the femora attributed to *Plesiorcyteropus* actually belong to a giant muroid. Deep patellar surfaces with high bounding ridges presumably function to constrain the excursion of the patella (and therefore the leg) when the vasti are forcibly contracted (Fleagle, 1988).

In distal aspect (fig. 33F), it may be seen that the condylar facets rapidly narrow in the anterior direction, and are separated from the distalmost part of the patellar surface by non-articular areas. In profile, the medial condylar facet is longer and more rounded than the lateral condylar facet. Although the facets themselves are large, the massive distal end of the femur projects to such a degree that they lie completely behind a line dropped through the posterior aspect of the shaft (fig. 33D). These facts, combined with the form of the facets, clearly show that the knee was incapable of full extension. Organization of the distal end of the femur is roughly similar in *Dasypus*, *Orycteropus*, *Meniscotherium*, and *Echinosorex*. *Tenrec* and *Tamandua* have comparatively smaller (less posteriorly projecting) condyles. *Bradypus* is quite different: the condyles are insignificantly projecting, the facets merge with the patellar surface, and as a consequence the leg is evidently capable of moving through a wider range of flexion-extension than is typically the case for other members of the comparative set.

The lateral condyle bears a small, proximolaterally positioned facet which apparently accommodated a lateral fabella (sesamoid of the gastrocnemius). There is no identifiable facet for a medial fabella.

The great anteroposterior depth of the distal end of the femur, combined with indications of large muscle masses for the knee extensors (e.g., size of origin of rectus femoris on the innominate), suggests that *Plesiorcyteropus* would have been able to generate considerable force against resistance when extending the leg to the degree permitted by articular surface morphology. This ability would be of value in bracing the body while digging, or in raising the trunk with the feet planted firmly on the substrate.

TIBIA AND FIBULA

The tibia and fibula are fused both proximally and distally in bibymalagasy and are conveniently described as a unit. Eight tibiofibulae, mostly incomplete, have been found in existing collections (MNHN 332, 335, 336/340, 337; MNHNA 1987.041, 042; NHMLP M 9946; USNMP 474082). The following descriptions are largely based on the Sirave specimen (MNHN 332), which is intact except for a fracture through the upper fibula (fig. 36; table 12).

There is a remarkable similarity in tibiofibular construction in bibymalagasy and armadillos (fig. 37, *Euphractus*). The strength of this resemblance was unwittingly recognized by Carleton (1936: pl. VI, fig. 2), who, not suspecting that the tibiofibula she studied actually belonged to *Plesiorcyteropus*, expressed the opinion that it was "of unknown type resembling armadillo." Lamberton (1946) noted several strong similarities to dasypodids: (1) the tibia and fibula are completely fused proximally and distally, the distal fusion being especially noteworthy because it involves almost one-fifth of the total length of the tibia; (2) the tibial shaft appears to be greatly compressed mediolaterally, a feature which is partly due to extraordinary enlargement of the tibial (cnemial) crest; (3) the distal articular surface is extremely narrow anteroposteriorly; and (4) the interosseous space is very wide. Nonetheless, he avoided drawing any conclusion from this evidence, other than to point out that there were fewer resemblances to *Orycteropus* and essentially none at all to manids and anteaters (fig. 37).

Patterson (1975) acknowledged the resemblances to dasypodids listed by Lamberton (1946), but dismissed them on the ground that the chief peculiarities of bibymalagasy tibiofibula are all replicated or foreshadowed within Orycteropodidae. Thus in *Orycteropus* (fig. 37) the tibial shaft is compressed, the interosseous space is wide, and the tibial crest is well developed, while in *Myorycteropus* a cnemial tubercle is found, and so on. Where no resemblance could be construed, Patterson (1975) retreated into teleology. For example, to overcome the interpretative difficulty that *Plesiorcyteropus*—but no true orycteropodid—displays distal tibiofibular

fusion, Patterson (1975: 215) maintained that as "regards the [distal] fusion, due to ossification of the interosseous membrane, *Plesiorhycteropus* has simply carried to conclusion a tendency latent in the family." Appeals to "latent tendencies" as a means of avoiding interpretative problems are not usually rhetorically successful, and in any case the tendency implied here—progressive ossification of the interosseous membrane—is simply irrelevant to the process. In mammals, interosseous membranes stretch between diaphyses; they do not extend onto epiphyses and joint capsules. Complete union of tibial and fibular epiphyses occurs only when continuous synchondroses are formed and maintained from the stage of cartilaginous anlagen onward (cf. rabbits; Craigie, 1948). All definite aardvarks for which there is material evidence, including *Leptorycteropus*, display the primitive, distally unfused condition (conditions in *Myorycteropus* are not known; MacInnes, 1956). The only *Orycteropus* specimen that I have examined that could be described as a partial exception is AMNH 51374, a robust female, in which the distal tibiofibular ligaments—but not the interosseous membrane—are heavily calcified.

The proximal end of the tibia of *Plesiorhycteropus* is transversely broad, with subequal condyles separated by a wide intercondylar space (fig. 36E). In addition to facets for the menisci themselves, which can be easily made out in MNHNP 332, posteriorly there is also a large facet for the cyamella (the sesamoid of the popliteus) occupying a distally directed extension of the lateral condyle (fig. 36B). Large cyamellae also occur in dasypodids and manids; a small one is present in *Orycteropus afer* (also the case in many primates, rodents, insectivores, carnivores, bats, and other edentates [Lessertisseur and Saban, 1967b]). In front of the medial condyle is an exceptionally prominent tubercle, quite separate from the very low intercondylar eminence, to which the anterior cruciate ligament presumably attached. A similarly distinct feature exists in *Orycteropus* and *Euphractus* (fig. 37); in *Manis* and *Tamandua* this area is continuous with the very well-developed intercondylar eminence, while in *Tenrec* it is not identifiable (fig. 37).

The tibial tuberosity, for insertion of the

patellar ligament, is present in all members of the comparative set, although it is negligible in *Manis* and *Tamandua* (fig. 37). *Orycteropus* has the most projecting tuberosity, while *Plesiorhycteropus* is intermediate in this respect. In *Plesiorhycteropus*, *Orycteropus*, *Meniscotherium*, and *Euphractus* the tibial tuberosity is continued distally as a raised crest (tibial crest) of exceptional definition. In *Tamandua* and *Tenrec* the crest is less well defined, while in *Manis* (in contrast to *Patriomanis*) a tibial crest cannot be differentiated from the general curvature of the anterior aspect of the tibia. In *Plesiorhycteropus*, the tibial crest terminates distally in the form of a large tuberosity, the cnemial tubercle (fig. 36A, D). The tubercle is of uncertain function, but it presumably received one or more of the tendinous expansions of the sartorius, semitendinosus, biceps, tenuissimus, and gracilis. If this interpretation is correct, these flexors of the leg clearly had a very distal point of insertion. *Phascogale* has a similarly positioned cnemial tubercle, onto which these muscles insert (Walker, 1967). *Thomomys* lacks a tubercle, but it does have very distal insertions of gracilis and semitendinosus (J. E. Hill, 1937). The cnemial tubercle, as an entity distinct from a widened tibial crest, is small or nonexistent in orycteropodids other than *Myorycteropus* (cf. Patterson, 1975), but is very large and prominent in *Meniscotherium* (somewhat less prominent in *Phenacodus*). Hyraxes have a low tibial crest that ends high on the tibia; at its distal end is a small cnemial tubercle (fig. 37).

Completely absent in *Plesiorhycteropus* is the large falciform process which springs from the anterior surface of the lateral condyle in *Orycteropus afer* (fig. 37). In *Plesiorhycteropus* the same area is sharp-margined, but otherwise unadorned, as is also true for all the other members of the comparative set. Patterson (1975) did not describe this process, but did mention the notch it creates by virtue of its slight separation from the tibial tuberosity. I assume that the aardvark's falciform process supports a muscular or fascial insertion (?part of biceps or ?iliotibial tract); it has not been described for any condylarthrans and I take it to be an autapomorphy of *Orycteropus afer* (and possibly other orycteropodids).

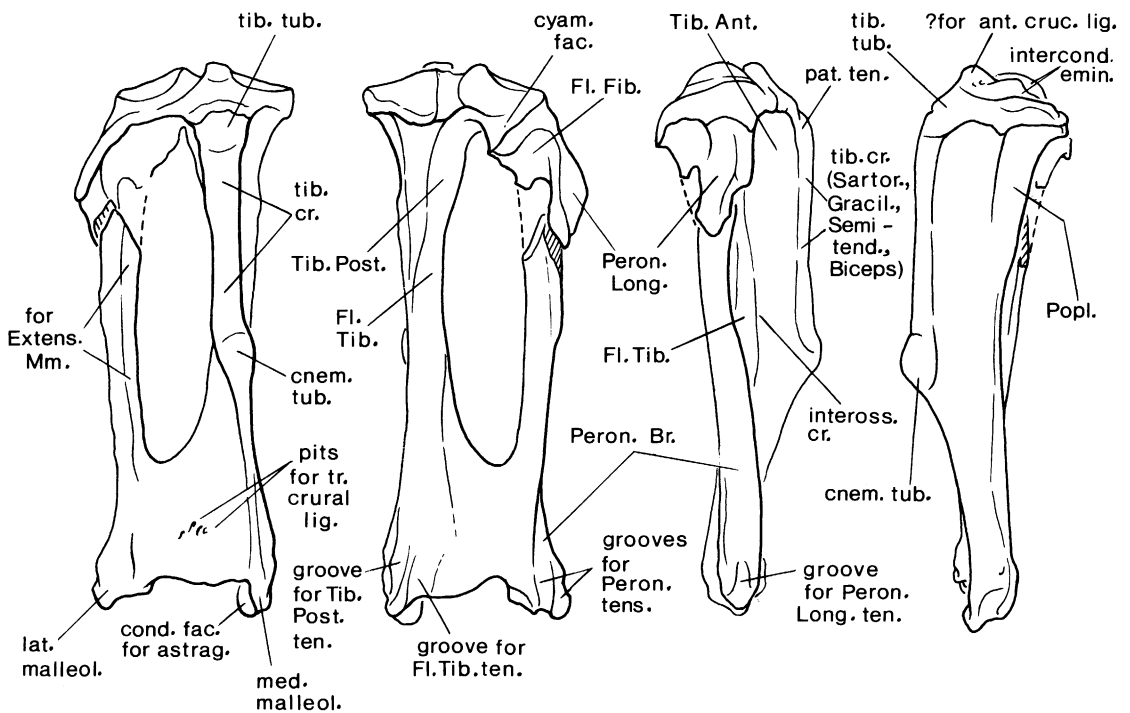
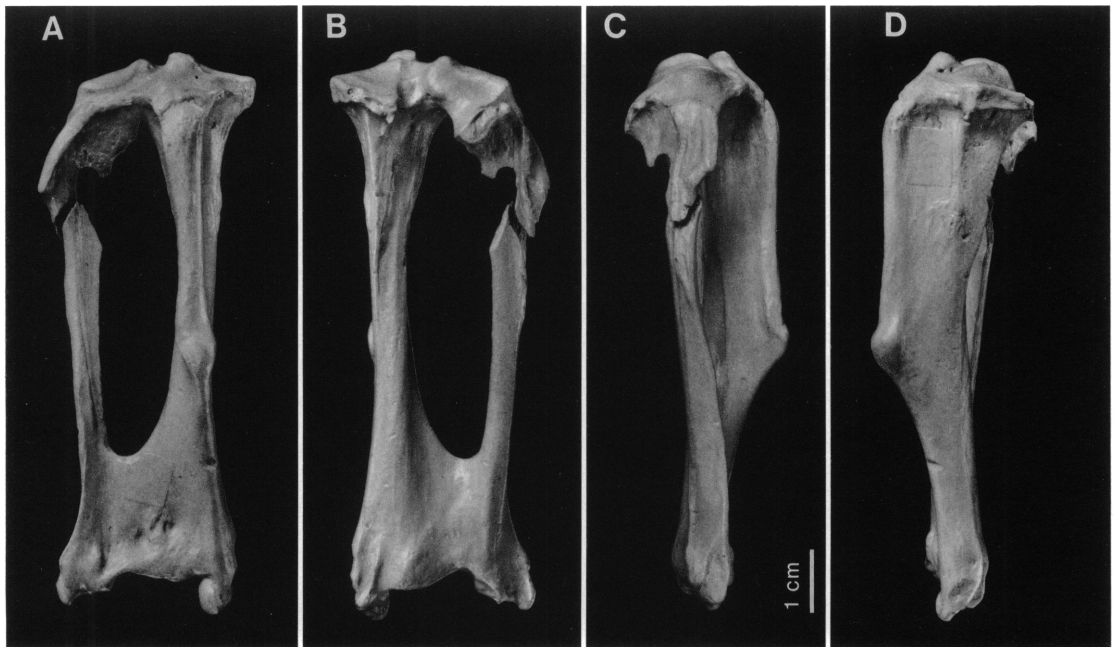


Fig. 36. Tibiofibula, *Plesiorycteropus* sp. MNHNP 332, right side. A, anterior; B, posterior; C, lateral; D, medial; E, proximal; and F, distal views. See keys. Square patches seen in A and D are original MNHNP labels glued to the specimen.

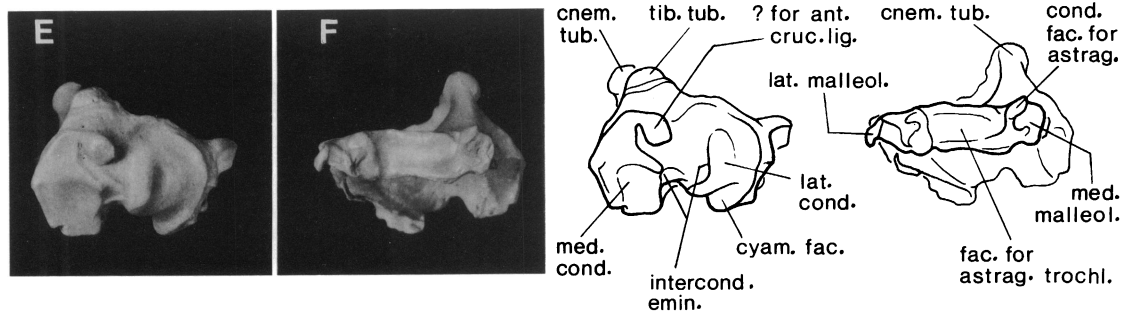


Fig. 36 (continued)

In lateral view (fig. 36C) the fibula in *Plesiorhycteropus* is oriented in nearly the same vertical plane as the tibia. In dasypodids the fibula is very strongly inclined relative to the tibia, so much so that the two bones describe an X when seen in lateral aspect (fig. 37, *Euphractus*). Less extreme cases of fibular inclination are seen in *Orycteropus* and *Manis*, while *Procavia*, *Tamandua*, *Tenrec*, and *Meniscotherium* resemble *Plesiorhycteropus* (see fig. 37 and Gazin, 1965). Correlated with the strong inclination of the fibula in dasypodids is the orientation of the distal articular surface. In most mammals, the proximal and distal articular surfaces of the tibia and fibula are oriented in the same coronal plane. In the case of dasypodids, however, the distal surface is set at about 60° to the proximal, with the result that (when examined in isolation) the lateral malleolus seems to jut out in front of the medial one. In armadillos the legs are not positioned under the body in normal walking posture, but are held akimbo, with the knees protruding laterally. As a result, the tibiofibula is obliquely angled, and, if the distal articular surface were oriented in the same transverse plane as the proximal surface, the feet would be splayed outward. Altering the set of the talocrural joint by moving the lateral malleolus forward (and thereby placing the fibula on a strong incline) undoes this effect, and permits the feet to face directly forward. Because *Plesiorhycteropus* agrees with the rest of the comparative set in having a normally oriented distal surface, it would appear unlikely that its distal hindlimb was positioned in the armadillo manner.

The distal end of the tibiofibula is dominated by massive lateral and me-

dial malleoli (fig. 36A). Despite the size of the lateral malleolus, the articular area for the lateral aspect of the astragalar trochlea is comparatively small. There is no evidence of a fibular facet for the calcaneum, despite the considerable distal projection of the lateral malleolus. Fibulocalcaneal contact, usually regarded as a primitive feature (but see Lewis, 1989), is found in monotremes, some marsupials, dasypodids, bradypodids, pholidotans, artiodactyls, proboscideans, and bats (Lessertisseur and Saban, 1967b). There is also a small contact in *Orycteropus*; unaccountably, Weber (1928) and Le Gros Clark and Sonntag (1926) stated that it is absent.

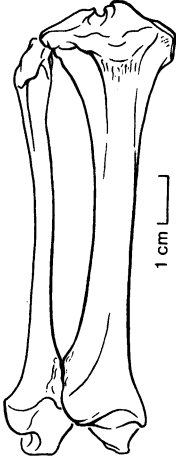
Part of the medial malleolus is transformed into a major articulating surface that engages the medial aspect of the astragalar neck (fig. 36A, F; see also fig. 40A). In most mammals with a well-developed medial malleolus, the structure's articulating surface is flat to slightly concave, laterally facing, and engages only the medial aspect of the astragalar trochlea—impinging little, if at all, on the astragalar neck. By sharp contrast, in *Plesiorhycteropus* the surface of the medial malleolus is markedly convex and anterolaterally facing, and articulates with a large, cupped facet (cotylar fossa) on the astragalar neck (fig. 40A). Approximations, slight or otherwise, to the condition found in *Plesiorhycteropus* are seen in hyraxes, *Orycteropus*, *Meniscotherium*, and a few other mammals. Full treatment of these matters is reserved for the description of the astragalus (see Cheiridia, Astragalus).

The numerous rugosities, grooves, and crests on the tibiofibula imply that the muscle masses responsible for moving the knee and ankle were of substantial size. In anterior as-

Orycteropus
afer



Manis
crassicaudata



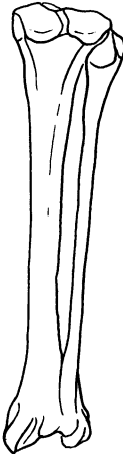
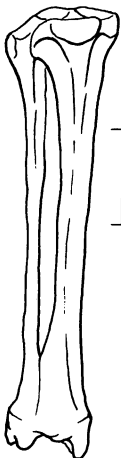
Euphractus
sexcinctus



Tamandua
tetradactyla



Tenrec
ecaudatus



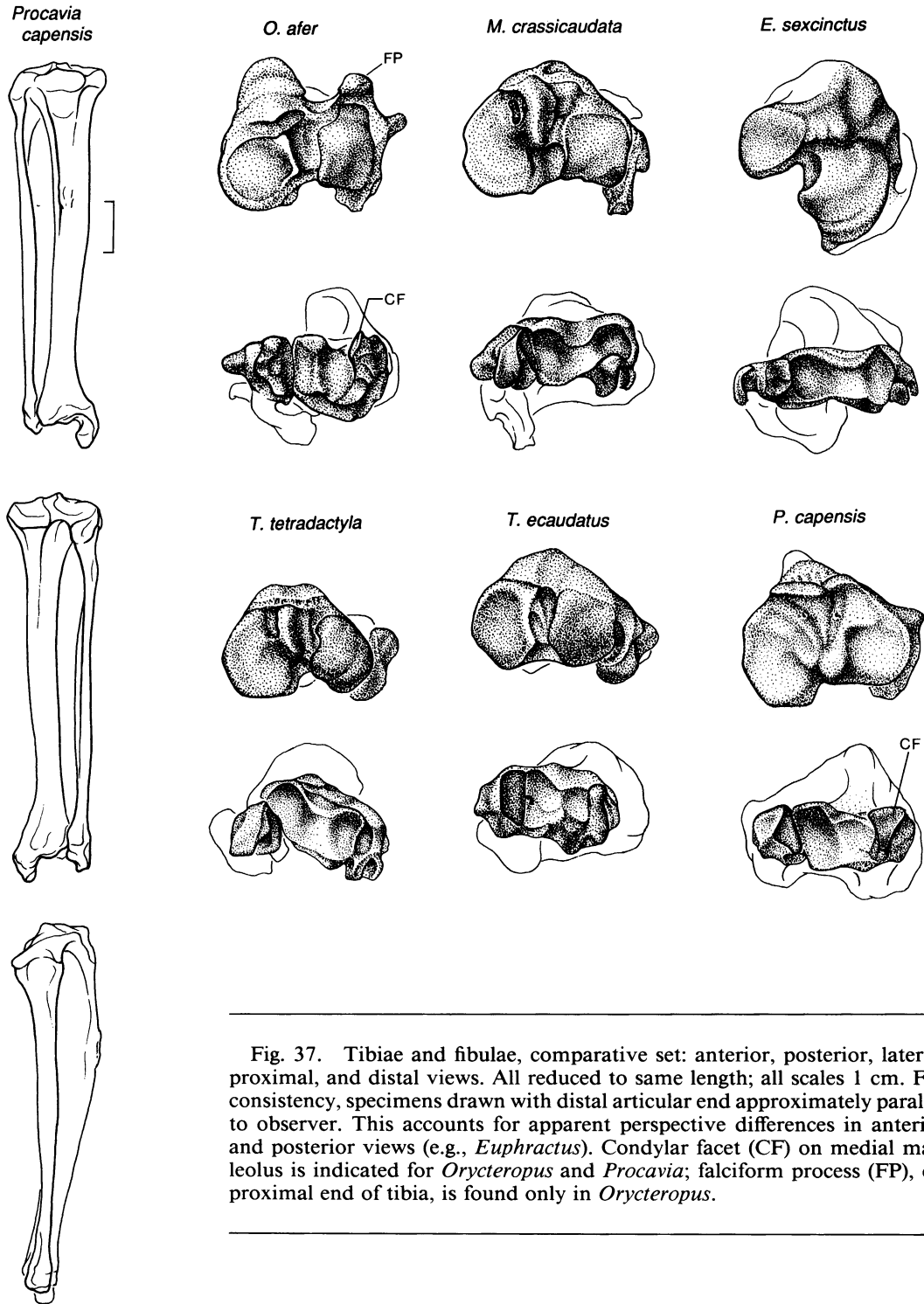


Fig. 37. Tibiae and fibulae, comparative set: anterior, posterior, lateral, proximal, and distal views. All reduced to same length; all scales 1 cm. For consistency, specimens drawn with distal articular end approximately parallel to observer. This accounts for apparent perspective differences in anterior and posterior views (e.g., *Euphractus*). Condylar facet (CF) on medial malleolus is indicated for *Orycteropus* and *Procavia*; falciform process (FP), on proximal end of tibia, is found only in *Orycteropus*.

pect (fig. 36A), the tibial tuberosity (for the patellar ligament and quadriceps) does not seem to be very prominent, but its lack of prominence is primarily due to the fact that it blends distally with the extremely large cne-mial crest. Tibialis anterior is normally the main dorsiflexor of the foot in unspecialized quadrupedal mammals, and constantly arises from the lateral aspect of the tibia and the adjacent part of the interosseous membrane and fibula. In *Dasypus* and *Orycteropus*, which have a proximal tibiofibular configuration similar to that of *Plesiorycteropus*, the bony origin of the tibialis anterior includes the deep fossa framed by the tibial crest and area of proximal fusion of the tibia and fibula (Galton, 1870). The large extensors of the digits (extensor digitorum longus, ext. hallucis longus) presumably arose from the anterior aspect of the fibula, although I have not attempted to identify scars for their origins in the figures. The anterior surface of the broad plate that forms the distal end of the diaphyseal part of the tibiofibula bears several large pits (fig. 36A) joined by rough crests. I infer that these pits mark the attachment site of a well-developed transverse crural ligament. This ligament, which prevents extensor tendons from bowstringing during foot dorsiflexion, tends to be well developed in diggers and is sometimes ossified (Reed, 1951).

On the posterior surface of the tibiofibula (fig. 36B), large muscle scars in the expected positions can be made out for popliteus, tibialis posterior, flexor digitorum fibularis (= flexor hallucis longus), flexor digitorum tibialis (= flexor digitorum longus), and peroneal musculature. Distally this surface presents four well-marked grooves, two on the tibial side and two on the fibular. I interpret the lateral grooves on the fibular malleolus as beds for the tendons of peroneus longus and brevis. The more medial of the two tibial grooves is presumably for the tibialis posterior, and the other, immediately lateral to it, is apparently for the flexor tibialis. Some uncertainty must attach to these identifications, inasmuch as flexor muscles are sometimes subdivided or reduplicated, with independent tendons (cf. Reed, 1951). Muscle sulci in these positions are frequently encountered in digging mammals (e.g., *Thomomys*, *Sca-*

panus, *Priodontes*) and are of no great moment. It may be noted, however, that *Orycteropus* lacks a clear separation of grooves for tibialis posterior and flexor tibialis.

Average tibial and femoral lengths (see table 13) yield a crural index of 0.79, indicating that the legs of bibymalagasy were short compared to their thighs.

CHEIRIDIA

At present, the only elements that can be referred to the bibymalagasy cheiridia are several astragali and a series of metapodials and phalanges assigned to the hand by Lamberton (1946). In my view, some of the metapodials and phalanges may belong to the foot rather than the hand; in any case, for convenience all of them will be described in this section.

ASTRAGALUS

There are four astragali in existing collections, but only three were mentioned by Lamberton (1946). Judging by his reported measurements, MNHNA 1987.044A (illustrated in Lamberton's pl. IV, fig. 2, 2a) and MNHNP 1655 are the specimens that he recovered at Sirave. A slightly larger specimen, MNHNP 1654, is apparently the unfigured specimen designated by Lamberton as having come from Ampasambazimba. MNHNA 1987.044B (figs. 38, 39) is from the Ampoza collection and I assume that this was the one not seen by Lamberton prior to the completion of his manuscript. Except for minor nicks and abrasions, the astragali are in excellent condition.

The astragalus of *Plesiorycteropus* can be characterized as squat, wide, and somewhat quadrilateral in form (fig. 38; table 12). The exceptionally broad but indistinct neck is laterally continuous with a wide buttress, here identified as the anterior shelf, that extends outward from the entire distal edge of the bone (fig. 38A). This shelf appears to have acted as a stop for the tibiofibula during extreme dorsiflexion, because the shelf's dorsal surface bears a deep fossa (fig. 38C) for reception of a prominent lip on the tibia's anterodistal margin. The keels of the trochlear

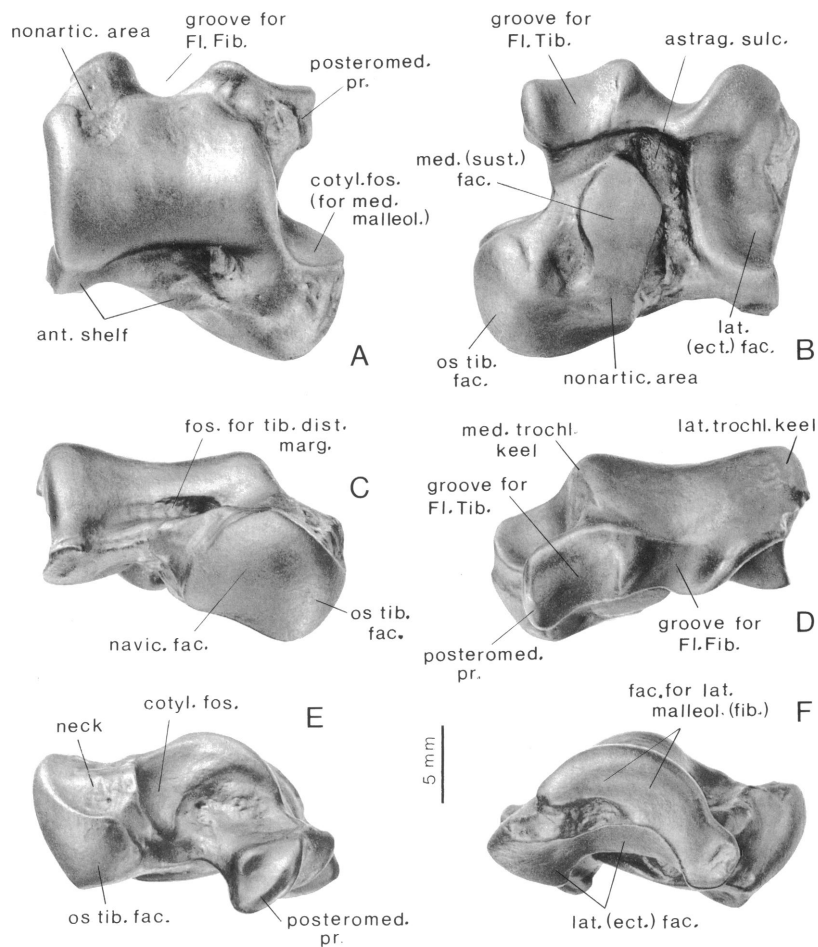


Fig. 38. Astragalus, *Plesiorycteropus* sp. MNHNA 1987.044B, right side. A, dorsal (crural); B, ventral (volar); C, distal (anterior); D, proximal (posterior); E, medial; and F, lateral views.



Fig. 39. Stereopair of astragalus illustrated in fig. 38, oblique dorsomedial view, to illustrate cotyloid facet for medial malleolus.

spool are very low, and the surface as a whole is broader laterally than medially (fig. 38A, D). Posteriorly, there is a significant nonarticular strip on the lateral side of the trochlear surface. The smooth, rounded appearance of the head in dorsal aspect (fig. 38A) is misleading; contra the impression given by Patterson (1975), the facet for the navicular is actually rather flat and faces directly anteriorly (fig. 38C). Roundedness in dorsal view is contributed by the large facet for os tibiale (i.e., the tarsal sesamoid in the tendon of tibialis posterior), from which the navicular facet is indistinctly separated by a low carina (fig. 38C). Close inspection of the lateral side of the head showed no indication of a facet for the cuboid in any specimen. The shortness of the neck and the absence of a cuboid facet suggest a serial rather than an alternating arrangement of the tarsus.

A singular feature of the *bibymalagasy* astragalus is the posteromedial process, a large excrescence on the internal aspect of the body, immediately behind the trochlear surface (fig. 38A, B, D). This process, not mentioned by Lamberton or Patterson, is present in all four astragali and shows no sign of having developed from a separate center. (So-called posterior processes of the astragalus are sometimes produced by the coalescence of a separate ossicle, os trigonum, with the body of the astragalus; such ossicles, however, are usually situated on the lateral side of the pathway of the flexor fibularis tendon [Lessertisseur and Saban, 1967b].) The underside of this process is deeply scored by a smooth-walled groove that opens obliquely upward (present in all specimens, but especially obvious in MNHNA 1987.044B). In fact, the groove's surface is so smooth that it suggests an articular surface. However, given its orientation and location, it is highly improbable that the posteromedial process articulated with anything. There is no evidence, in my view, that this process contacted the substrate, i.e., that it acted as an auxilliary support for the medial side of the foot.

The other, and more plausible, argument is that the groove is related to the passage of a tendon, and that it therefore acted as a pulley for one of the extrinsic flexors of the foot, thereby substantially increasing the outforce.

The likeliest occupant of the groove is the tendon of flexor tibialis, because there is a matching groove on the tibia immediately above the posteromedial process (fig. 36B). The adjacent tendon of flexor fibularis presumably passed into the foot in the usual way, in the groove on the posterior aspect of the astragalar trochlea (figs. 38A, 40B). I assume, but obviously cannot demonstrate, that the tendon of tibialis posterior ran along an anatomical plane that did not intersect the posteromedial process.

The lateral and medial calcaneal articular facets are roughly parallel in orientation, and are set at a slight oblique to the long axis of the body (fig. 38B). The lateral (ectal) facet is deeply concave. The medial (sustentacular) facet is positioned almost centrally, at a significant distance from the medial margin of the ventral surface. This facet is mediolaterally narrow and much smaller than the lateral facet. Anteriorly, it is separated from the plantar edge of the navicular facet by a small nonarticular strip (contra Lamberton [1946], who stated that the two facets were in contact). The posterior part of the medial facet is essentially planar; it does not slope downward to form a hook for embracing the posterior wall of the sustentaculum. The short length of the facet indicates a restriction of sliding movement along the medial side of the subtalar joint.

The astragalar foramen as a complete channel is absent, as Lamberton (1946) and Patterson (1975) noted. However, on the ventral surface of each specimen, tucked under the posterior border in the floor of the astragalar sulcus (fig. 38B), there is a small foramen that opens into the substance of the astragalus. Following Lamberton, I take this to be the incompletely obliterated remnant of an astragalar foramen that existed in early ontogeny.

The articular facet for the lateral malleolus is small, subvertical and essentially flat (fig. 38F). The facet for the medial malleolus (figs. 38, 39) has a more complicated morphology. Part of the malleolar facet is situated in the usual location, on the medial aspect of the trochlea; it does not extend onto the posteromedial process (fig. 38E). The rest of this facet, however, continues onto the astragalar

neck, where it spreads and deepens into a cup. As noted earlier, the cup (hereafter, cotylar fossa) receives the hemispherical or condylar articular surface developed on the medial malleolus. The cotylar fossa is separated by a wide interval from the posteromedial process.

Astragali of extant members of the comparative set are on the whole quite unlike that of *Plesiorhycteropus* (figs. 41, 42; C 28, 29), although some taxa require comment. Patterson (1975) considered the bibymalagasy astragalus to be "specialized" in comparison to those of *Orycteropodids* and *condylarthrans*, but did not comment on similarities and differences in any detail. Compared to *Plesiorhycteropus*, in *Orycteropus* (fig. 41) the trochlear keels are distinct and much higher, the fibular articulation is much better developed, the neck is more distinct, the navicular articular surface is subspherical, and there is a complete astragalar foramen. At the same time, however, the malleolar facet impinges on the astragalar neck to a small extent and there is a strong posteromedial process. In *Orycteropus* the cotylar facet is practically coplanar with the medial keel of the trochlea, but in bibymalagasy the facet is much deeper and set at a near right angle to the medial keel. The posteromedial process of the aardvark astragalus is also different in that it seems to be primarily articular: the medial part of the talocrural joint surface extends on it, and there is no discernible gutter for a muscle tendon on its underside. Finally, the shape and disposition of calcaneal facets is quite similar in the two taxa.

The manid astragalus (fig. 42) bears a deeply concave navicular facet (also seen in myrmecophagids), long neck, restricted and contorted trochlear surface, and single articular facet for the calcaneus. In agreement with the bibymalagasy astragalus, armadillo astragali (fig. 42) possess a low trochlear surface, flattened navicular surface, restricted fibular facet, and small, centrally placed sustentacular facet; but the medial keel is better developed, the facet for the medial malleolus is not cotyloid, and there is no hint of the anterior shelf or the posteromedial process.

In general there are no important correspondences to lipotyphlans, although it is of

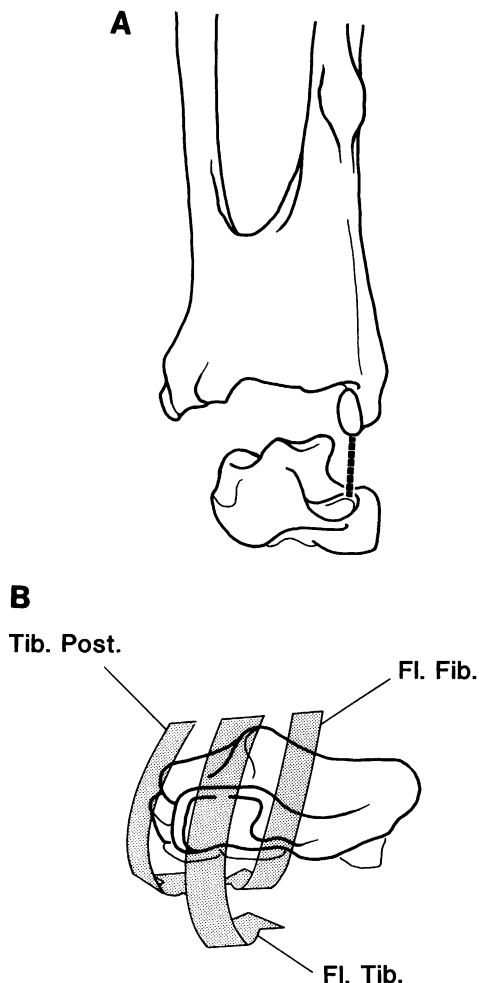


Fig. 40. Features of astragalus and tibiofibula of *Plesiorhycteropus*. A, Articulation (dashed line) of medial malleolus and astragalus, exploded view as seen from anterior aspect. B, Inferred placement of major tendons crossing posterior aspect of astragalus. Note in particular the tendon of flexor tibialis traveling in groove on posteromedial process.

some interest that the posterior aspect of the astragalus of some soricomorphs is scored by a deep, smoothwalled common flexor groove (e.g., *Crociodura*). The result is not really much like the groove on the posteromedial process of *Plesiorhycteropus*, however, because it is not held away from the body of the astragalus on a separate excrescence and grooves for flex-

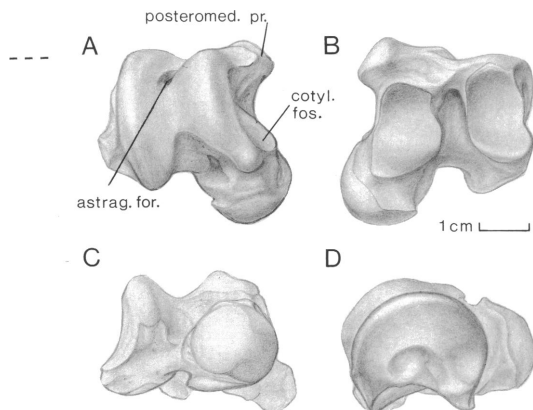


Fig. 41. Astragalus of *Orycteropus afer* in A, dorsal; B, ventral; C, distal; and D, lateral views.

ores tibialis and fibularis are not separate. The size and orientation of the head are radically different in *Tenrec* (fig. 42).

Finally, although there are few detailed resemblances between the astragali of *Plesiorhycteropus* and hyracoids, both bear deep cotylar fossae (Jouffroy, 1971c; Rasmussen et al., 1990). This is not, however, as rare a feature as some commentators think (see fig. 56; C 28).

METAPODIALS

Although the highly distinctive metapodials (figs. 43–46) attributed to *Plesiorhycteropus* cannot be confused with those of any other Malagasy mammal, very few of them have turned up in collections. Lamberton (1946) identified only five (MNHP 1656, 1657; MNHNA 1987.044C–E), all from Sirave, and attributed them to the manus. To these I add MNHNA 1987.044F, from Ampoza, and USNMP 474083, lately collected by Helen James and David Burney at Anjohibe (see Material, Taxonomy, and Occurrence).

The Ampoza specimen (fig. 46) is of significance for several reasons. Its medial and lateral sides possess well-developed facets for articulation with adjacent metapodials, which means it must represent an interior digit. However, it is much smaller than any of the metapodial specimens described by Lamberton. One way of explaining the apparent size discrepancy is to assume that the Ampoza

specimen is a metacarpal, in which case the Sirave elements could be metatarsals. Another possibility is that the digital rays in the hands (and perhaps the feet) of bibymalagasy varied in length and robusticity, as is commonly the case in highly fossorial mammals. If *Plesiorhycteropus* was a digger, as much of the postcranial evidence already discussed appears to indicate, it would seem only reasonable to infer that its hand (and possibly its foot) was armed with at least one large and specialized interior digit capable of energetic excavation (cf. hypertrophied MC 3 and MT 3 of manids, MC 3 of myrmecophagids, MC 3 of *Metacheiromys*). Against this argument is the fact that enlarged metapodial elements of a distinctive sort referable to *Plesiorhycteropus* have not turned up (or have not been recognized) in paleontological sites. For the present I see no reliable way of separating hand from foot bones, although in the following paragraphs I make suggestions for some elements based on considerations of comparative morphology.

Lamberton identified the elements now numbered MNHP 1657 (fig. 43) and MNHNA 1987.044E as “MC” 2, and MNHNA 1987.044C (fig. 44) and 1987.044D as “MC” 4. He considered his remaining specimen, MNHP 1656 (fig. 45), to be the “MC” 5. MNHNA 1987.044E and 1987.044D come from the same side of the body, but their bases cannot be brought into articulation and therefore Lamberton was correct in inferring that neither of them can represent the third metapodial.

Lamberton thought that the first metacarpal was probably absent in bibymalagasy, as it is in orycteropodids, although he cited no useful evidence to support this argument. The much smaller specimen from Ampoza, MNHNA 1987.044F (fig. 46), cannot be a first or fifth metapodial because it bears well-developed proximal facets on both sides. It is therefore from either the second or fourth digital rays.

As a group, all of the available elements are short relative to their breadth, with broad, obliquely angled distal surfaces and narrow proximal surfaces. Each of these elements is pronouncedly asymmetrical through its long axis, one side of the shaft being distinctly

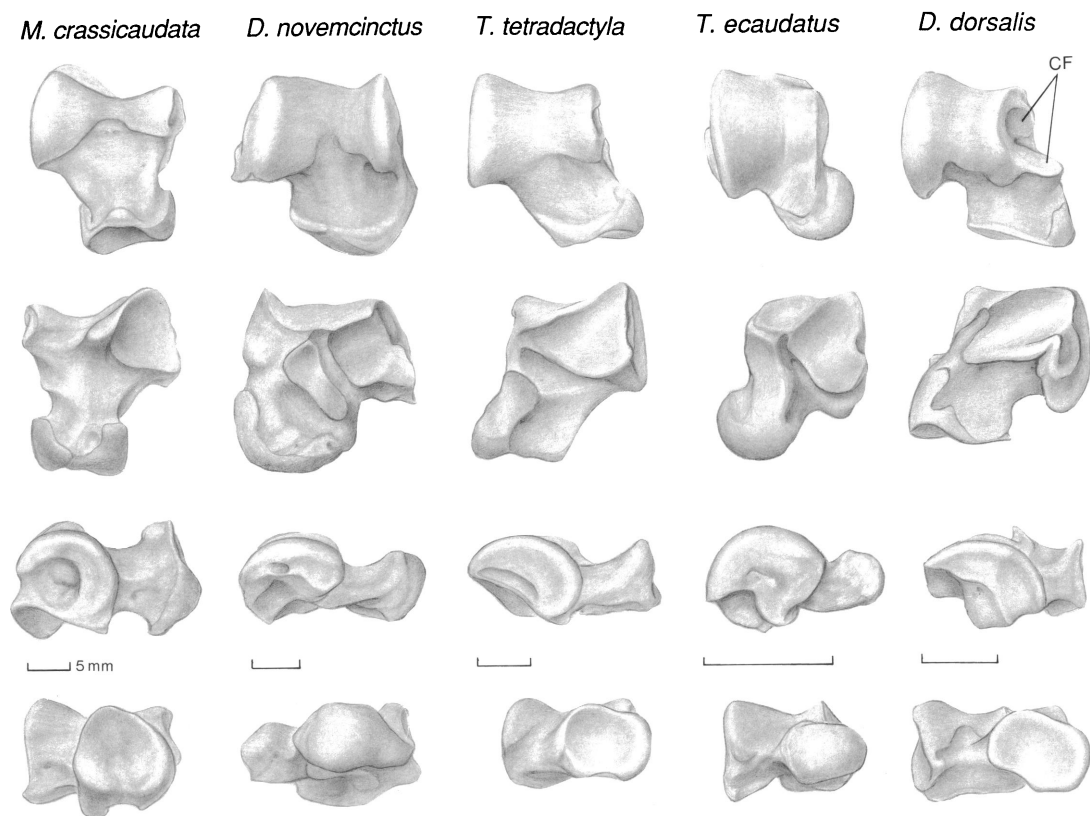


Fig. 42. Astragali, comparative set: dorsal, ventral, lateral, and distal views. All reduced to same length; all scales 5 mm.

more concave than the other. Their heads are also asymmetrical, being notably sloped to one side when seen in dorsal or plantar aspect. If elements considered to be "MC" 2 and 4 by Lamberton are correctly identified as to position within the cheiridium, then their distal ends evidently pointed away from the axis of the unknown third digit (cf. figs. 43, 44). This could imply, as Lamberton (1946: 45 [trans.]) surmised, that these collateral digits fanned out around the (presumably large) third digit—"a common disposition in edentates," he remarked. Lamberton also noted that the metapodial heads possess a prominent central spline that is completely restricted to the ventral side of the joint surface, as in dasypodids. By contrast, in manids, anteaters, and orycteropodids in particular the spline extends onto the dorsal surface of the metapodial as well.

From a morphological standpoint the most

interesting and bizarre metapodial element is MNHNP 1656, which Lamberton took to be "MC" 5—if it were not MT 5 or MT 1 (fig. 45). The specimen is very short and robust, and bears a facet for another metapodial on only one side. This last fact indicates that it must have been from an exterior digital ray, either the medialmost or the lateralmost element in its series. Its shaft is much more robust than that of MNHNA 1987.044F, which suggests that it should be associated with the elements that Lamberton identified as metacarpals (i.e., MNHNA 1987.044C, D, E, and MNHNP 1657). However, it does not articulate well with 1987.044D, the apparent "MC" 4 from the same side of the body. USNMP 474083 is from the opposite side but is otherwise morphologically indistinguishable from the MNHNP specimen.

The element's most peculiar feature is the large process, equal to approximately one-

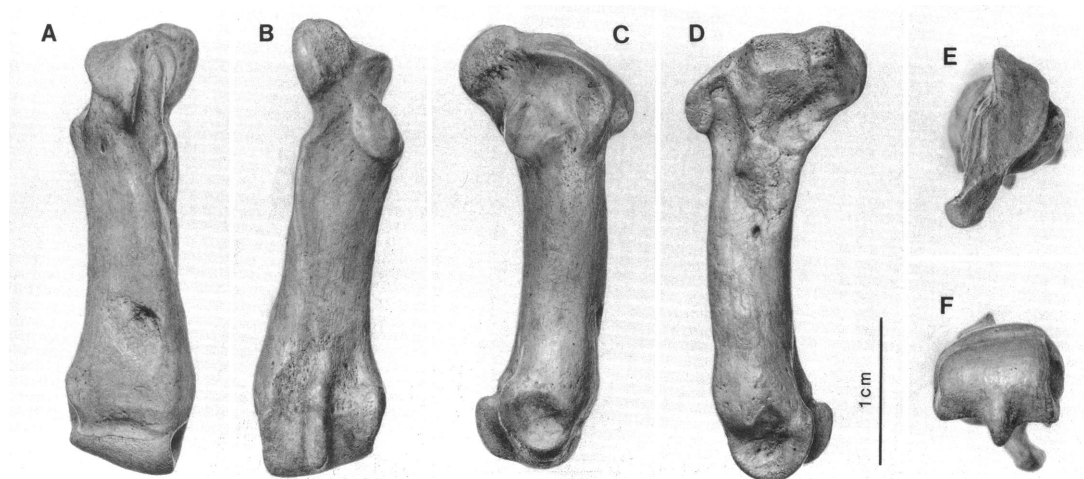


Fig. 43. Metapodial (?second) of *Plesiorycteropus* sp. MNHNP 1657. A, dorsal; B, plantar; C, side; D, opposite side; E, proximal; and F, distal views.

third of the shaft length, which projects from the plantar aspect of the base. Although one's first impression is that the process may be a greatly enlarged tubercle for the peroneus brevis like that seen on the MT 5s of some mammals (e.g., *Phascodomys*), it cannot be homologous with that structure because it bears a small but distinct facet near its tip (articular facet on process, fig. 45C). If one assumes that the element represents MT5 but that the process is on the element's medial

side, then it might be argued that this outgrowth received the tibialis posterior insertion. However, I know of no mammal having a tibialis attachment site of equivalent size. Similarly, in mammals the MC 5 and MC 1 seemingly never produce an unusually prominent process in this position for the intrinsic flexors. (When large attachment sites do occur, the sites are usually on the prepollex or hamate.)

Another reason for rejecting the identifi-

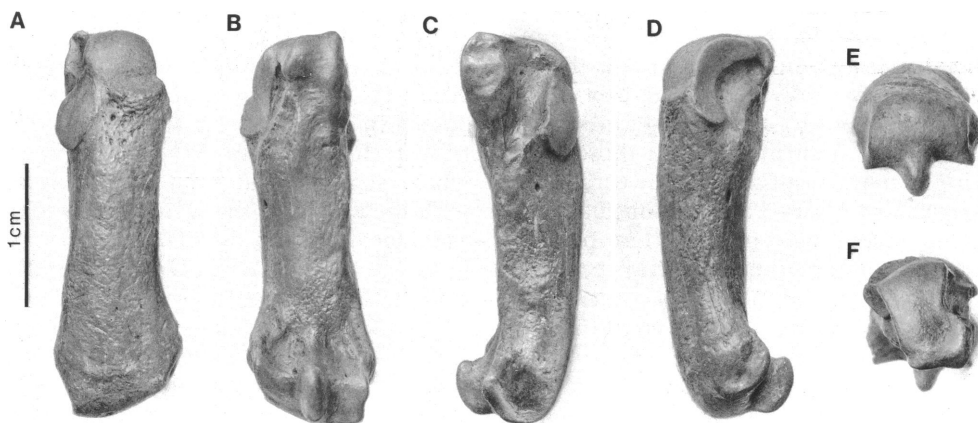


Fig. 44. Metapodial (?fourth) of *Plesiorycteropus* sp. MNHNA 1987.044C. A, dorsal; B, plantar; C, side; D, opposite side; E, distal; and F, proximal views.

cation of MNHNP 1656 as either MT 5 or MC 5 is its proximal articular facet (fig. 45A), which has a complicated concavo-convex surface that spreads partway down the large process (fig. 45E). This joint-surface shape is not typically seen in mammalian MT/MC 5s, because the cuboid or hamate facet tends to be subplanar, even in instances in which the metapodial in question is greatly hypertrophied (e.g., *Phascolomys*).

Alternatively, if MNHNP 1656 is regarded as a left MT 1, the proximal facet would have articulated with the medial cuneiform, which frequently possesses a saddle-shaped articular surface. The large process—of no interpretable function—would then have pointed laterally and proximally, and the small articular facet on its end might have articulated with MT 2 (although I was unable to produce a convincing contact with the putative second metapodials, 1657 and 1987.044E). Against this identification is the point noted by Lamberton, which is that the head is sloped even more strongly than in the other metapodials discussed above—an unlikely morphology for a first metatarsal. At present I see no other reasonable possibilities: in my view, the element is simply too well-formed and typically metapodiallike to entertain the argument that it may represent either a prehallux or a prepollex.

PHALANGES

The element now numbered MNHNP 1658 was described and illustrated by Lamberton (1946: pl. 4, fig. 6) as a proximal phalanx of *Plesiorycteropus*. I question this identification. The proximal articular surface of this specimen is symmetrically concave and unnotched, whereas proximal phalanges articulating with any of the identified metapodials would have to be both asymmetrical and proximally notched in order to fit the sloped male surfaces and splines on these bones. Lamberton (1946) met these objections by assuming that MNHNP 1658 articulated with the unknown third metapodial, which he thought may have possessed a more symmetrical head than the metapodials that flanked and converged upon it. He explained the absence of a groove to accommodate the spline by inferring that the habitual posture

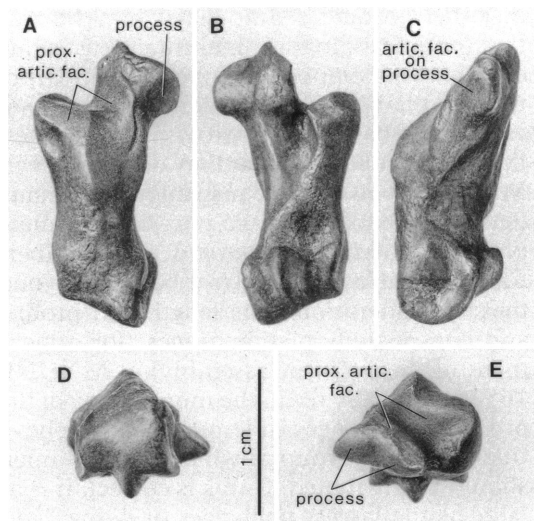


Fig. 45. Metapodial (?first or fifth) of *Plesiorycteropus* sp. MNHNP 1656. A, dorsal; B, plantar; C, side; D, distal; E, proximal views.

of the digit was such that the carena did not encroach upon the phalanx (?if posture were digitigrade).

Since no third metapodials of bibymalagasy have been identified, Lamberton's explanations cannot be directly tested. However, his assessment strikes me as unlikely

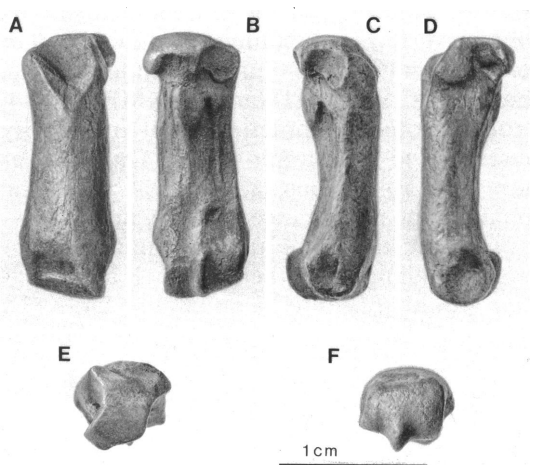


Fig. 46. Metapodial (?metacarpal), *Plesiorycteropus* sp. MNHNA 1987.044F. A, dorsal; B, plantar; C, side; D, opposite side; E, proximal; and F, distal views.

on other grounds. Although it may be true that in some digitigrade mammals (e.g., some carnivores) metapodial splines do not participate in the MCP joints and therefore do not groove the bases of the proximal phalanges, the usual situation is that they do. Moreover, MNHNP 1658 differs conspicuously in many details of shape from the two ?intermediate phalanges of *Plesiorycteropus* that Lamberton (1946) also identified (see below). Beyond these considerations, the length, flat profile, and conspicuous plantar ridges (for attachment of the extensor assembly) of MNHNP 1658 specifically recall the morphology of the proximal phalanges of lemurs, and I believe that this is the group to which this specimen should be attributed. If this is correct, it is as large as the largest phalanges of living *Indri* and must belong to this taxon or some extinct one in a similar size range.

In size and details of shape, MNHNA 1987.044G and H (figs. 47A–D) are not like the phalanges of any known mammalian group represented in Madagascar, and by exclusion may be regarded as belonging to *Plesiorycteropus*, as Lamberton (1946) argued. These elements are exceptionally short and squat. The cupped, asymmetrical proximal articular surfaces are deeply incised by a wide embrasure on the plantar margin. Because of the sharply inclined orientation of the proximal facets, dorsal length of diaphyses is shorter than plantar length. Their distal articular surfaces are somewhat different: that of 1987.044G has a typical, rounded profile, but that of 1987.044H (and USNMP 474084, from Anjohibe) is practically flat and mostly restricted to the plantar aspect. This last feature is very curious, and almost gives the phalanx the appearance of a tiny hoof. However, since there are already candidates for distal phalanges (see below), such an allocation would appear to be untenable. Dr. K. D. Rose (personal commun.) has pointed out to me that MNHNA 1987.044H resembles proximal phalanges of the palaeonodont *Alocodontulum*, while MNHNA 1987.044G is reminiscent of an intermediate phalanx of the same taxon (cf. Rose et al., 1992). Although no phylogenetic relationship is posited between *Plesiorycteropus* and *Alocodontulum*, the similarities are indeed compelling and I identify these phalanges accordingly in figure

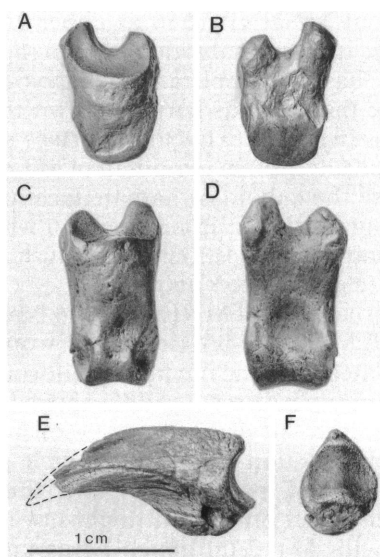


Fig. 47. Proximal, middle, and distal phalanges of *Plesiorycteropus* sp. A, B, dorsal and plantar views of MNHNA 1987.044H; C, D, dorsal and plantar views of MNHNA 1987.044G; E, F, side and proximal views of MNHNA 1987.044K.

47. This means that proximal phalanges were shorter than middle phalanges in *Plesiorycteropus*. In *Orycteropus afer* this proportion occurs only in the digital ray of MC 5, although it is not uncommon among diggers (Hildebrand, 1985).

Identification of the unguals of bibymalagasy is problematic. Lamberton (1946) assigned several phalanges characterized by their narrow profile and clawlike form to *Plesiorycteropus* (fig. 47E, F) but did not discuss why this allocation was feasible. However, they can be convincingly articulated with MNHNA 1987.044G, a possible intermediate phalanx, and in any case they are either too large or of the wrong shape to belong to any of the native viverrids, tenrecs, or nesomyines. In being small and highly compressed they differ radically from the more massive unguals characteristic of energetic diggers, and the apparent lack of mortise-and-tenon construction in distal interphalangeal joints stands as a major difference from the complex joint surfaces preventing hyperextension which are seen in anteaters, pangolins, and armadillos. It may be, of course, that these particular distal phalanges are from

digital rays that did not play an important role in digging. This problem was not directly addressed by Lamberton (1946), who merely concluded that the long, arching claws that capped these phalanges could have functioned in tree climbing as well as digging. Bibymalagasy unguals differ in profile from the deep, arched claws of highly arboreal mammals and correspond more to those found in fossorial taxa in exhibiting long, shallow shafts, curving dorsal surfaces, and reduced extensor tubercles (cf. MacLeod and Rose, 1993). Scansorial mammals are similar except that, on average, the extensor tubercle is better developed. (There are, however, important exceptions to this observation, such as fully arboreal *Coendou*; cf. MacLeod and Rose, 1993.)

I will briefly note here that I considered the possibility that the tegulate phalanges that Lamberton (1946) assigned to *Plesiorhycteropus* actually belong to a large bird. However, Helen James (USNM), who kindly examined casts of these specimens, concluded that they were not avian.

Patterson (1975) had little to say about the metapodials and phalanges of *Plesiorhycteropus*, and if he was disturbed by their many departures from conditions in *Orycteropus* his text does not reflect it. Instead, he concentrated on noting departures from manid conditions, such as the absence of fissuring in bibymalagasy unguals.

FUNCTION, ADAPTATION, AND EXTINCTION

The further an extinct animal departs from any identifiable extant analog, the more difficult it becomes to develop plausible and defensible functional reconstructions for it. With respect to one major adaptation—digging—*Plesiorhycteropus* does not represent an interpretatively problematic case, because the evidence for it is reasonably conclusive. Nevertheless, the skeletal evidence also presents us with a number of traits that seem paradoxical—or at any rate unexpected—in a committed digger. These features suggest that the bibymalagasy skeleton was adapted for more than one kind of major biological role, and identifying these roles is important for completing the morphological portrait of *Plesiorhycteropus* offered here.

BODY SIZE

Although body size and its implications do not play an important role in the interpretations presented in this section, in view of the general significance of body size in determining an animal's requirements and life history (Damuth and MacFadden, 1990) some estimates of size may prove useful to other workers.

In the absence of associated skeletons of *Plesiorhycteropus*, body weight estimates have to be based on inferences from isolated spec-

imens. Table 14 presents estimates using femoral cross-sectional areas, following the methodology of Ruff (1987; see also Biewener, 1982). Biknevicius and Ruff's (1992) technique was used to take cross-sectional areas at the 35% position on radiographs of MNHNP 329 (assigned to *P. germainepetterae*) and MNHNA 1987.038 (assigned to *P. madagascariensis*). These are, respectively, the smallest and largest femora in the hypodigm. Obviously, it is not known whether they are representative of their respective species.

Ruff's (1987) analysis was limited to primates. In view of the unsettled affinities of *Plesiorhycteropus*, it is of interest to compare estimates developed from more than one kind of eutherian mammal. Log-transformed cross-sectional areas were inserted into regression expressions developed from two additional data sets (caviomorph rodents, and a manid/dasypodid composite). The caviomorph regression model produced values substantially higher than those of the manid/dasypodid and primate models (table 14). On the whole, I am disposed to accept the lower estimates because *Dasypus kappleri* and *Euphractus sexcinctus*, whose femoral shapes and dimensions are similar to those of bibymalagasy species, weigh on the order of 6–7 and 9–10 kg, respectively (Wetzel, 1985).

TABLE 14
Plesiorycteropus: Body Weight and Brain Size Estimates

	Small Femur MNHNP 329 (ref. <i>P.</i> <i>germainepetterae</i>)	Large Femur MNHNA 1987.038 (ref. <i>P.</i> <i>madagascariensis</i>)		
1. Femur, cortical cross-sectional area (in mm ²) ^a	62.29	92.46		
2. Weight estimation models (in kg): ^b				
Caviomorph model	10.83	18.37		
$L_{10}BW = -1.13598 + 1.3343(L_{10}CA)$				
$r^2 = 0.98$				
Manid/dasypodid model	6.24	9.64		
$L_{10}BW = -1.1781 + 1.0998(L_{10}CA)$				
$r^2 = 0.88$				
Primate model	7.81	13.22		
$L_{10}BW = -1.496 + 1.331(L_{10}CA)$				
$r^2 = 0.99$				
3. Indices of cranial capacity for <i>Plesiorycteropus germainepetterae</i> (method of Martin, 1990) ^c				
	BW (g)	C_A (cm ³)	C_E (cm ³)	ICC
Caviomorph model	10,830	17	17.93	0.95
Manid/dasypodid model	6240	17	12.32	1.35
Primate model	7810	17	14.35	1.18

^a Femora measured at the 35% position (i.e., point equal to 35% of total bone length, measured from distal end).
^b BW, body weight in kg; CA, cortical cross-sectional area. Caviomorph and manid/dasypodid sets were assembled by Audrone Biknevičius; for primates, regressions developed by Ruff (1987) were used directly. All data are derived from adult, wild-collected specimens of known body weight.
^c BW, body weight in grams; C_A , empirical cranial capacity (in cm³), equivalent to amount of water displaced by endocast of MNHNP 327; C_E , estimated cranial capacity (in cm³), as predicted by expression $L_{10}C_E = 1.51 + 0.68(L_{10}BW)$; ICC, index of cranial capacity = C_A/C_E .

Yet it should be noted that estimated brain size using the caviomorph model yields a value (17.93 cm³) that is very close to empirical size (17 cm³), while the other two models underestimate it (table 14). Clearly, satisfactory weight estimates will have to await the discovery of articulated specimens. Extant *Orcyteropus* weighs 40–100 kg (Shoshani et al., 1988). There are no weight estimates for *O. gaudryi*, but the articulated skeleton (AMNHP 22762), no larger than that of a medium sized dog, suggests a weight of 20 kg or less. One of the poorly known Siwalik tubulidentates, *Orycteropus browni* (Colbert, 1935), may have been even smaller.

CORRELATES OF DIGGING

Bibymalagasy possessed many of the attributes that typify mammals specialized for

scratch-digging (Hildebrand, 1982, 1985). This is especially obvious in the forelimb, the excavation tool of most vertebrate diggers. In scratch-digging, the forefeet are first extended over the substrate, then the digits are powerfully flexed. This drives the claws into the soil or other substrate, which is then broken as the forefeet are drawn back toward the body (cf. Thewissen and Badoux, 1986). Short distal forelimb elements, marked distances between muscle origins/insertions to increase moment arms, and relatively large muscle masses as reflected by rugosities and long lever arms—all adaptations frequently seen in diggers for increasing or controlling outforce at the distal ends of the forelimb—are osteologically detectable to a greater or lesser degree and can therefore be examined in fossil evidence (cf. Coombs, 1983; table 15). Forelimb traits of *Plesiorycteropus* that

TABLE 15
Development of Selected Characters in Digging Mammals (after Coombs, 1983)^a

	<i>Myrmecophaga</i>	<i>Taman- dua</i>	<i>Manis</i>	<i>Orycteropus</i>	<i>Priodontes</i>	<i>Mar- mota</i>	<i>Tachyglossus</i>	<i>Vombatus</i>	<i>Plesio- rycter- opus</i>
Low brachial index									
0, >91; 1, 90–76; 2, <75	0	1	2	2	2	0	0	1	2
Low intermembral index									
0, >81; 1, 80–71; 2, <70	0	0	1	2	2	1	0	1	2
Large acromion	2	2	0	2	2	2	0	1	?
Long, prominent deltopectoral crest	2	1	2	2	2	0	1	2	2
Wide entepicondyle of humerus	2	2	2	2	2	2	0	2	2
Long, prominent supinator crest	1	1	1	1	2	1	0	2	1
Long olecranon process									
0, <20% of ulna; 1, 20–29%; 2, >30%	1	0	1	2	2	0	0	1	2
Short, wide metacarpals	1	1	2	0	2	1	2	2	2?
Long sacrum fused firmly to pelvis	2	2	2	0	2	0	2	1	0
Short or absent pubic symphysis	2	2	2	2	2	0	2	2	2
Long or large tail	2	2	2	2	2	1	0	0	2

^a 0, little/no development of character; 1, moderate development; 2, extreme development. Coombs' (1983: fig. 1) codings for all taxa except *Plesiorhycteropus*.

may be described as adaptations for digging include: (1) radius shorter than humerus (low “average” brachial index; cf. table 13); (2) metapodials short and wide (to the extent known); (3) proximal/intermediate phalanges short and wide (to the extent known); (4) prominent, distally elongated deltopectoral crest; (5) wide medial epicondyle, for pronators and carpal/digital flexors; (6) well-developed, proximally extensive supinator crest, for long extensors and supinator; and (7) long olecranon (triceps) process, to increase leverage of triceps and dorsiepitrochlearis (as reflected in high olecranon indices; cf. table 13). There are other forelimb traits correlated with digging such as short manus, long acromion, and long pisiform (cf. Coombs, 1983), but these cannot be evaluated because of lack of material.

With respect to the trailing end of the body, in vertebrate diggers the hindlimb and tail act to brace the body, shovel away the spoil, or both (Hildebrand, 1985). Traits frequently seen in diggers and also documented in *Plesiorhycteropus* include: (1) long hindlimb compared to forelimb, (2) short or absent pubic symphysis, and (3) large or long tail. A low

intermembral index (“average” of 0.61 in *Plesiorhycteropus*; table 13) is to be expected in diggers, in view of their propensity to reduce relative forearm length. Reduction of the pubic symphysis occurs in many diggers, although the functional basis for this trait remains obscure (Hildebrand, 1985). The tail was certainly wide in bibymalagasy, judging from the size of the transverse processes of anterior caudals (fig. 20), and was probably long as well, although its length cannot be estimated from available evidence.

Finally, it may additionally be noted that stabilization of joints is exceptionally important in diggers because of the great forces generated during fossorial activity. Consequently, diggers have developed a number of adaptations to prevent or limit unfavorable motions at affected joints (Hildebrand, 1985). These frequently include: (1) limitation in range of motion at joints that primitively allow motions in several planes; (2) strengthening, against dislocation, of joints providing motion in one plane; (3) passive mechanisms to prevent hyperextension of hinge joints; and (4) enhancement of rigidity by loss or fusion of bones. Although the morphology of the

wrist and elbow joints of *Plesiorhycteropus* suggests that mobility was limited compared to that of nondiggers, there is less indication of this than in most other fossorial mammals. This is especially obvious in the case of the distal ulna, which is not expanded—in contrast to virtually all other diggers. Known metapodial heads are equipped with splines which would have acted to strengthen metapodial-phalangeal joints, although the splines themselves are limited to the ventral surfaces of the heads, in contradistinction to anteaters and armadillos, in which the splines extend over to dorsal surfaces. Phalangeal morphology suggests that, when quadrupedal, *Plesiorhycteropus* bore most of its weight on metapodial heads. As discussed earlier (see Radius), the power to bring the hand into full pronation may have been limited by the nature of the joint surfaces involved in the proximal radioulnar joint, although in quadrupedal posture bibymalagasy could have compensated for this limitation by medially rotating and possibly abducting the humerus, as *Tamandua* does (Taylor, 1978) and *Meniscotherium* may have done (Gazin, 1965: 55). It is also possible that *Plesiorhycteropus* actually walked with its hand in the midprone position, by resting its body weight on the ulnar side of its hand or on the dorsal intermediate phalanges (cf. *Manis*; Kingdon, 1974). The existence of good mobility at the shoulder is indicated by the position of the humeral head in relation to the tuberosities, a feature which is paralleled in the pocket gopher, *Thomomys* (J. E. Hill, 1937).

CORRELATES OF POSTURE AND LOCOMOTION

Not all diggers display the same suite of adaptations for digging in the same way (Coombs, 1983); moreover, some diggers possess adaptations for other, quite different biological roles (e.g., climbing or general arboreal activity in smaller manids and vermilinians). *Plesiorhycteropus* has some notable skeletal features that appear to relate not so much to locomotor activity per se as to posture. These attributes may relate, of course, to some unknown aspect of bibymalagasy digging behavior, although other interpretations are possible. Despite the elu-

siveness of a credible functional interpretation for these features, they are interesting enough to warrant the following short treatments.

VERTEBRAL ADAPTATIONS

Plesiorhycteropus displays two specializations of the lumbar region that occur in certain species that frequently assume sitting or other truncally erect postures. These specializations concern the dimensions of the neural arch in the posterior part of the spine (posterior thoracics to posterior lumbers). They involve (1) caudal increase in transverse width combined with (2) caudal decrease in anteroposterior length of the neural arch (NAT and NAW, table 9). Increasing the transverse width of the neural arch moves the pedicles of the zygapophyses further apart; decreasing the anteroposterior length brings pre- and postzygapophyseal facets closer together. Since the functional importance of this arrangement relates to the separation of zygapophyseal facets (Jenkins, 1974), it would have been desirable to measure distances between the facets themselves. Unfortunately, zygapophyses are rarely well preserved in the bibymalagasy vertebral sample, so the dimensions of the neural arch were used instead. I find that the distance between the centers of postzygapophyseal facets on lumbar vertebrae matches up tolerably well with the minimum transverse width of the neural arch. For this reason, I will refer to postzygapophyseal separation in the following paragraphs even though in some cases the measurement used to express separation is neural arch transverse width. Pertinent comparative measurements are provided in tables 16 and 17.

Primitive conditions can be explored with reference to *Tenrec ecaudatus*, a quadrupedal eutherian without conspicuous lumbar specializations. (For a useful collection of illustrations of the vertebral column in representative mammals, consult Owen [1851].) In *Tenrec*, the degree of transverse separation between postzygapophyses (= neural arch transverse width) is essentially uniform through the lumbar series, as ratios of last to first lumbers (PLu/ALu) and last to middle lumbers (PLu/MLu) illustrate (table 16). Also

TABLE 16
Comparison of Transverse Widths of Neural Arches (NAT) of Selected Lumbar Vertebrae of
Plesiorcyteropus and Some Other Mammals^a

Taxa	PLu/ALu (or PLu/PTH)	Prop. factor: ^b	PLu/MLu	Prop. factor:
<i>Homo sapiens</i>	57.2/24.9 (Lu5/Lu1)	2.30	57.2/28.3 (Lu5/Lu3)	2.02
<i>Ursus americanus</i>	52.5/35.1 (Lu6/Lu1)	1.50	52.5/35.3 (Lu6/Lu3)	1.49
<i>Plesiorcyteropus</i> sp. ^c	22.9/15.8 (Lu6/Lu1)	1.41	22.9/18.0 (Lu6/Lu3)	1.27
<i>Orycteropus afer</i>	28.3/23.9 (Lu7/Lu1)	1.18	28.3/24.3 (Lu7/Lu4)	1.16
<i>Orycteropus gaudryi</i>	20.1/18.3 (Lu8/Lu2)	1.10	20.1/17.3 (Lu8/Lu4)	1.16
<i>Papio anubis</i>	29.6/27.0 (Lu7/Lu1)	1.10	29.6/29.7 (Lu7/Lu4)	1.00
<i>Presbytis johnii</i>	15.6/14.7 (Lu6/Lu1)	1.06	15.6/15.6 (Lu6/Lu1)	1.00
<i>Manis javanica</i>	14.5/13.8 (Lu6/Lu1)	1.05	14.5/14.7 (Lu6/Lu3)	0.99
<i>Meniscotherium terraerubrae</i>	14.0/13.5 (Lu7/Lu1)	1.04	14.0/14.0 (Lu7/Lu4)	1.00
<i>Erythrocebus patas</i>	16.4/17.1 (Lu7/Lu1)	0.96	16.4/16.2 (Lu7/Lu4)	1.01
<i>Tenrec ecaudatus</i>	7.2/7.5 (Lu5/Lu1)	0.96	7.2/7.5 (Lu5/Lu1)	0.96
<i>Priodontes maximus</i>	22.9/24.4 (Lu2/Th13)	0.94	22.9/24.4 (Lu2/Lu1)	0.94
<i>Phascolarctos cinereus</i>	12.5/14.0 (Lu8/Lu1)	0.89	12.5/13.1 (Lu8/Lu4)	0.95
<i>Geomys bursarius</i>	4.5/6.1 (Lu7/Lu1)	0.74	4.5/4.7 (Lu7/Lu4)	0.96
<i>Procyon capensis</i>	5.9/8.9 (Lu8/Lu1)	0.66	5.9/8.0 (Lu8/Lu4)	0.74

^a Measurement NAT defined in table 9. For some specimens, value for NAT represents separation between postzygapophyseal facets per se; for others, separation of pedicles supporting postzygapophyses. Sample size: N = 3 for each extant taxon (means only). Values for *Orycteropus gaudryi* AMNHP 22762 and *Meniscotherium terraerubrae* AMNHP 48002 based on mounted specimens with significant amounts of reconstruction, and their validity is uncertain. *Meniscotherium* mount includes only seven lumbar, although nine or ten lumbar are known to have existed in *M. chamense* (Gazin, 1965; Williamson and Lucas, 1992).

^b Prop. factor = proportion of two vertebrae indicated. Taxa ranked on basis of PLu/ALu (PLu/PTH in case of *Priodontes*, which has only two lumbar). Abbreviations: ALu, anterior lumbar; MLu, middle lumbar; PLu, posterior lumbar; PTh, posterior thoracic.

^c *Plesiorcyteropus* specimens (from table 9): Lu1, average of MNHNA 1987.043K and L; Lu3, MNHNP 542; Lu6, MNHNP 541.

TABLE 17
Comparison of Anteroposterior Widths of Neural Arches (NAW) of Selected Lumbar Vertebrae of
Plesiorcyteropus and Some Other Mammals^a

Taxa	PLu/ALu (or PLu/PTH)	Prop. factor:	PLu/MLu	Prop. factor:
<i>Erythrocebus patas</i>	9.9/16.7 (Lu7/Lu1)	0.59	9.9/17.8 (Lu7/Lu4)	0.56
<i>Homo sapiens</i>	13.0/21.4 (Lu5/Lu1)	0.61	13.0/21.5 (Lu5/Lu3)	0.60
<i>Plesiorcyteropus</i> sp.	6.1/9.3 (Lu6/Lu1)	0.66	6.1/8.6 (Lu6/Lu3)	0.71
<i>Papio anubis</i>	12.9/18.0 (Lu7/Lu1)	0.72	12.9/20.1 (Lu7/Lu4)	0.64
<i>Ursus americanus</i>	35.2/43.5 (Lu6/Lu1)	0.81	35.2/45.2 (Lu6/Lu3)	0.78
<i>Orycteropus gaudryi</i>	12.5/15.2 (Lu8/Lu2)	0.82	12.5/14.9 (Lu8/Lu4)	0.84
<i>Tenrec ecaudatus</i>	5.3/6.0 (Lu5/Lu1)	0.88	5.3/6.7 (Lu5/Lu1)	0.79
<i>Procyon capensis</i>	6.5/7.3 (Lu8/Lu1)	0.89	6.5/8.3 (Lu8/Lu4)	0.78
<i>Orycteropus afer</i>	23.5/24.7 (Lu7/Lu1)	0.95	23.5/25.2 (Lu7/Lu4)	0.93
<i>Meniscotherium terraerubrae</i>	12.1/12.5 (Lu7/Lu1)	0.97	12.1/11.9 (Lu7/Lu4)	1.01
<i>Phascolarctos cinereus</i>	14.2/14.0 (Lu8/Lu1)	1.01	14.2/13.8 (Lu8/Lu4)	1.03
<i>Priodontes maximus</i>	31.5/29.4 (Lu2/Th13)	1.07	31.5/31.8 (Lu2/Lu1)	0.99
<i>Myrmecophaga tridactyla</i>	23.3/21.0 (Lu2/Th16)	1.11	23.3/22.2 (Lu2/Lu1)	1.05
<i>Presbytis johnii</i>	15.4/13.7 (Lu6/Lu1)	1.12	15.4/15.6 (Lu6/Lu3)	0.99
<i>Manis javanica</i>	16.5/14.0 (Lu6/Lu1)	1.17	16.5/15.5 (Lu6/Lu3)	1.06
<i>Geomys bursarius</i>	5.9/5.0 (Lu7/Lu1)	1.18	5.9/6.0 (Lu7/Lu4)	0.98

^a Measurement NAW defined in table 9; for notes on specimens, definitions, and abbreviations see table 16.

essentially constant is neural arch width (table 17), although there is a slight tendency for the width of the arches of middle lumbar to increase (also here considered primitive). In these and many other features, the lumbar of *Tenrec* are highly homomorphic, exhibiting little or no morphological or functional differentiation. A lumbar spine with these characteristics is primarily adapted for dorsoventral loading, with the spine held more or less constantly in the horizontal position.

There are many departures from this primitive pattern in the comparative set, and squeezing these variations into general categories is probably dangerous. However, with respect to the first character of interest, postzygapophyseal separation (table 16), two extremes may be defined. The first may be termed "keystoning," in which postzygapophyseal separation decreases caudad and therefore produces low proportional factors (< 1.00). In the comparative set, keystoning does not seem to be uniquely correlated with a particular locomotor style (cf. *Geomys* vs. *Procavia*), and indeed a wider range of comparisons indicates that moderate keystoning is a widely distributed feature.

The opposite and much more restricted adaptation is "splaying," in which the separation between postzygapophyses tends to caudally increase through the lumbar series (proportional factors > 1.00). Among extant terrestrial mammals, the most exaggerated form of postzygapophyseal splaying (2.30) occurs in *Homo sapiens*, in correlation with increasing size of lumbar bodies in this species. The effect of these adaptations in humans is to better dissipate the high cranio-caudal loads that accompany locomotor postures normally assumed by humans (Cartmill et al., 1987). Large splays also occur in some animals which are known to occasionally assume postures involving truncal uprightness, such as bears (e.g., *Ursus americanus*). *Plesiorycteropus* exhibits values for postzygapophyseal separation that are only slightly less than those recorded for *Ursus*. The value for PLu/ALu (1.41) in bibymalagasy is open to challenge, because the elements compared do not come from the same animal, but this objection does not apply to the slightly lower PLu/MLu value (1.32), which is based on the Ambolisatra partial

skeleton. Other examined taxa exhibit considerably lower values, including the cercopithecines *Papio*, *Presbytis*, and *Erythrocebus*, despite the fact that these primates are quite capable of sitting and assuming other truncally upright postures.

Another adaptation of *Homo* that appears to be correlated with truncal erectness and axial loading is the dramatic caudal decrease in craniocaudal width of lumbar neural arches (table 17), obvious in any dorsal view of the articulated human spine (e.g., Warwick and Williams, 1973: fig. 3.51). In most mammals, lumbar neural arches vary little in width; in fact, many species show a tendency to increase the width of the last lumbar arch, which is the opposite of the human condition. Substantial caudad decline in arch width is noticeable in only a few nonhuman mammalian taxa; the only ones that can be so classified in table 17 are *Erythrocebus*, *Plesiorycteropus*, *Papio*, and (to a lesser extent) *Ursus*. Arch narrowing is correlated with lumbar lordotic curvature in *Homo*, and it could be argued that this adaptation facilitates throwing the lower part of the human spine into its characteristic reverse curve (i.e., enhances lumbar extension). However, lordosis in humans is due less to bony morphology than to differences in the dorsal and ventral widths of intervertebral disks (Warwick and Williams, 1973), and, in any case, this curve is absent or negligible in bears (Davis, 1964) and Old World monkeys (Schultz, 1930). Here it may be noted that cervicothoracic lordosis, of the sort described for dasyrodids, some digging insectivores, and the palaeonodont *Dipassalus* (Rose et al., 1991), is not associated with lumbar modifications of the kind encountered in *Plesiorycteropus*.

The only behavioral denominator shared by the living taxa seems to be the frequent assumption of truncally upright postures (comprising sitting, bough-straddling, occasional standing, and so on in the case of the bears and monkeys). Old World monkeys are evidently not uniform, as more arboreal *Presbytis* displays a much higher value than ground-dwelling *Erythrocebus* and *Papio*. As to *Plesiorycteropus*, bipedalism in the human sense is completely out of the question, given the direction of the foramen magnum, shape of the pelvis, form of the articular surfaces

of the lower limbs, and many other traits. On the other hand, the ability to extend the lumbar spine through a substantial range of motion might help a short-limbed, relatively heavy animal like *Plesiorhycteropus* assume a tripod posture, with the tail acting as a supporting strut.

Another item of importance is the relationship between the height and breadth of the lower free vertebrae. This increases in a specific manner in humans (Slijper, 1946): the last lumbar is typically the shortest and broadest, and exhibits the widest separation of the postzygapophyseal facets. Parallels to this are also seen in ground-living Old World monkeys (Gregory, 1920) and in ricochetal rodents (Hatt, 1932). Sample limitations complicate interpretation of conditions in *Plesiorhycteropus*, although it does appear that cross-sectional areas of vertebral bodies substantially increase through the lumbar part of the column. For *Homo*, these last features are plausibly interpreted as part of a complex for the safe and efficient transmission of the weight of the upper body to the pelvis and lower limb in bipedal posture. For Old World monkeys, the correlation is not with locomotor posture (which is habitually quadrupedal in most of the taxa considered here), but instead with a resting posture in which the trunk is vertically implanted over the pelvis. Given the shortness of the astragalus and all other known cheiridial bones in *Plesiorhycteropus*, ricochetal locomotion can be discounted as an explanation for the vertebral modifications encountered in bibymalagasy.

The combination of substantial craniocaudal increase in postzygapophyseal separation, equally significant decrease in neural arch width, and increase in cross-sectional areas of lumbar centra is not encountered in any xenarthran, pholidotan, or lipotyphlan. Among the members of the comparative set, aardvarks may be said to be closest to bibymalagasy in morphology. This is true as far as it goes and is reflected in the proportionate factors in tables 16 and 17, but the gap is a large one. Measurements for *Orycteropus gaudryi*, which because of its small body size is a more pertinent comparative case than *O. afer*, are closer to *Tenrec*—and therefore to the inferred primitive condition—than to *Plesiorhycteropus*.

The only condylarthran that merits special mention here is *Meniscotherium*, because Gazin (1965) specifically noted that in this taxon the posterior thoracics and lumbar display a “surprising increase” in size. Unfortunately, he did not supply any measurements of these vertebrae, and his figures do not really suggest a dramatic size increase of the sort seen in *Plesiorhycteropus*. Measurement of the mounted skeleton *Meniscotherium terraerubrae* AMNH 48002 indicates only a slight increase in centrum depth between the first and last lumbar, while NAW and NAT vary very little (tables 16, 17). It is also obvious from Gazin’s (1965) figure 8 that neural arch craniocaudal width does not significantly decrease caudad in *M. robustum*—indeed, it appears to increase up to the middle lumbar, and then to slightly decrease thereafter. Additional confirmation of these points comes from the measurements of *M. chamense* provided by Williamson and Lucas (1992, their table 4), who show that centrum dimensions are greatest in the middle lumbar region.

On the evidence presented so far, it seems reasonable to conclude that bibymalagasy exhibit morphological attributes of the lumbar that appear to be connected with enhancement of extension, withstanding of craniocaudal compression, or both. Such features do not appear to be basic to digging adaptations, since they are rare or absent in extant diggers. On the other hand, these adaptations would certainly augment the ability of any basically quadrupedal animal to practice some form of truncal erectness, either habitually or occasionally. For the sake of completeness it should be mentioned that the function of the vasculature of the transarcual canals (see Vertebral Column) may relate to reallocation of venous return in certain postures (cf. discussion by Barnett et al. [1958] regarding functional aspects of extradural venous supply in various mammals). However, in view of our ignorance concerning what these canals actually transmitted, speculation on this point seems useless.

PELVIC ADAPTATIONS

One pelvic character of bibymalagasy that demands a functional explanation is the re-

markable transformation of the ischial tuberosities into smooth-surfaced triangular plateaus, the ischial expansions (see Innominate). In many mammals, some portion of the caudal surface of the ischium is normally free of muscular attachments and therefore in contact with the skin and subdermal tissues, but this portion is normally as rugose as the rest of the tuberosity. Thus the bibymalagasy ischial expansion cannot simply be dismissed as a device to permit the skin of the haunch to glide freely.

The only extant mammals whose ischial configurations strongly resemble that of bibymalagasy are cingulate xenarthrans and certain anthropoid primates (fig. 32). In dasypodids the expanded ischial tuberosities act as platforms for the support of the carapace, and hence their most important correlate is armoring. By contrast, in gibbons and cercopithecoid monkeys, the functional correlate is postural, the equivalent areas being fashioned into large plaques which provide backing for the "sitting pads" or ischial callosities. For completeness it may be noted that the ischial tuberosities of a few other extant mammals (e.g., ursids, geomyids, leporids, vombatids, *Tragulus*) may be described as slightly to moderately expanded, but they do not match those of armadillos or Old World monkeys in special features such as the absence of rugosities. Among fossil mammals not related to cingulates or cercopithecoids, expanded ischia seem to be very rare (or perhaps rarely described). One instructive example is the schizotheriine perissodactyl *Chalicotherium*, which has somewhat wider ischial tuberosities than do other chalicotheres. Zapfe (1979), who identified this feature, argued that its presence implied that *Chalicotherium* frequently assumed sitting postures while browsing.

While it does not follow from the foregoing that the ischial expansions of *Plesiorcyteropus* must have supported either armor or sitting pads, these are the likeliest analogs and therefore deserve brief comparative treatment.

ARMORING

In armadillos, the expanded caudal surface of the ischium is clearly a design feature for

carapace support, because it is present in all dasypodid taxa and varies in size and other characteristics according to body mass (fig. 32). In the small three-banded armadillo *Tolypeutes* (1.5 kg; Wetzel, 1985), the ischial territory involved in the contact is small and oblong (4.0×6.1 mm in *T. matacus* AMNHM 248394). In the larger six-banded armadillo *Euphractus* (5.4 kg; Wetzel, 1985), this territory is a raised, smooth-surfaced ledge that extends rostrally to the level of the last sacral foramen (21×5 mm in *E. sexcinctus* AMNHM 70092). The contact zone in the giant armadillo *Priodontes* (29 kg; Wetzel, 1985) is a more exaggerated version of the one seen in *Euphractus*; it is a massive, flattened, medially flared protuberance that extends up to the transverse level of the second-last sacral foramen. *Euphractus* and *Priodontes* also exhibit broadened surfaces for carapace support on the sacral spinous processes and dorsal aspects of the ilia. Lamberton's (1946: pl. II) illustrations of the Ambolisatra pelvis give the impression that the ischial expansions faced directly caudally. This is due to the angle at which the pelvis was photographed, and is misleading; in life the ischial expansion would have faced dorsocaudally (fig. 32).

Although the position and orientation of the expanded ischial tuberosity are roughly similar in *Plesiorcyteropus* and middle-sized armadillos like *Dasypus kappleri*, I am unable to adduce any convincing morphological evidence for the presence of a bony carapace in bibymalagasy. Dermal ossicles are frequently encountered in Malagasy subfossil sites, but in all the ones that I have seen are attributable either to the crocodile *Crocodylus* or the tortoise *Aldabrachelys*. If bibymalagasy had possessed dermal ossifications, these surely would have shown up before now. (In South American sites containing armored xenarthrans, dermal ossicles are many times more abundant than their jaws or other skeletal remains [cf. Simpson, 1931]). Elongated metapophyses exist in *Plesiorcyteropus*, but unlike their counterparts in dasypodids in the same body-size range, they are not apically flattened and their size decreases rather than increases caudad (cf. Owen, 1851).

The other possibility that merits discussion is that the ischial expansions of *Plesiorcyter-*

opus supported some form of armoring that did not involve a bony carapace. The only pertinent models among extant mammals seem to be the formation of scales in pholidotans and the elaboration and ossification of connective tissue structures in the pelvic area of chevrotains. (Localized skin thickenings are found in diverse locations in a number of mammals [Sokolov, 1982], but they have no known osteological correlates and are therefore paleontologically inaccessible.)

Manid scales are unossified and keratinous, but they are heavy: Kingdon (1974) estimated that in pangolins the skin and scales alone comprise 20% or more of live weight. To move these structures, pangolins have developed specialized dermal muscles not found in other mammals (Jouffroy, 1966, 1971a), but these leave no impressions on bones. Unlike armadillo carapaces, the scale mass of pangolins does not appear to require a specialized bony support structure in the pelvic area (other than that indicated by general skeletal massiveness). Thus in *Manis gigantea*, whose live body weight of 16 kg is one-third skin and scales (Kingdon, 1974), the ischial tuberosity is only slightly expanded. I do not know if the moderate dorsal thickenings on the ilium and the peculiar, elevated transverse processes of the last sacral of pangolins qualify as armor supports, although the well-developed metapophyses of the lower thoracics and the lumbar have been so interpreted (Lessertisseur and Saban, 1967b). *Plesiorhycteropus* lacks dorsal thickening of the ilium, and on none of the preserved vertebral metapophyses is there dorsal flattening or anteroposterior elongation of the sort seen in at least the larger extant species of pangolins. Some of the weight estimates in table 14 could be taken to mean that *Plesiorhycteropus* had a very bulky body for its linear size, but beyond this there is little that implies a manidlike external form.

Connective tissue underlying the skin of the dorsum and flanks of male and female *Tragulus* forms a thick meshwork of highly organized fibers (Dubost and Terrade, 1970). This feature is correlated, apparently in aged males only, with extensive ossification of fascial sheets and ligaments in the pelvic area (thoracolumbar, deep gluteal, crural fascia,

and ischiosacral ligament). Milne-Edwards (1864) gave these ossified sheets the evocative name "buckler" (*bouclier*) and found that they were attached to the iliac crest, spinous processes of sacral vertebrae, dorsal margin of the (ossified) sacrospinous ligament, and ischial tuberosity. My observations on a male chevrotain with buckler preserved (*Tragulus javanicus* AMNHM 90913) basically agree with those of Milne-Edwards. The caudal aspect of the ischial tuberosity in this animal is distinctly flattened, although it is not as relatively large as the equivalent flattened area in *Plesiorhycteropus*. The buckler is mostly composed of ossified deep gluteal aponeurotic tissues. Since these tissues run between different parts of the pelvic complex, the limitations on motion dictated by their ossification are probably minor. It should be noted that despite its martial name, the buckler seems quite useless for any protective purpose since the thickness of the ossified plate is only a fraction of a millimeter. Finally, the difficulty in drawing any parallels with pelvic organization in *Plesiorhycteropus* is that the chevrotain buckler leaves little osteological sign of its presence. In cleaned skeletons of *Tragulus* females and young males, there is little or no indication of incipient ossification at attachment sites for fasciae and ligaments.

Keratinous scales and ossified connective tissues are poor candidates for fossilization, and therefore their alleged existence in extinct forms is conjectural in all but a few cases (e.g., *Eomanis*, *Pholidocercus*; Storch, 1978).

SITTING

If ischial expansions in bibymalagasy had nothing to do with the support of external armoring, they may have helped instead to support the weight of the trunk in certain postures, as similar structures do in some primates. In the typical case in Cercopithecidae (e.g., *Macaca*), the modified ischial tuberosities have the shape of slope-shouldered right triangles (fig. 32). The dorsal side of each tuberosity is defined medially by a low eminence for the sacrotuberous ligament and laterally by a larger projection, to the periphery of which the hamstrings are attached. The surface of the tuberosity is slightly convex, uniformly but not markedly roughened, and

free of muscular attachments. The ischial callosity, composed of fibro-fatty cushions enclosed by a greatly thickened epidermis, is anchored to the ischial periosteum by fibrous septa (M. Rose, 1974). The cushioning properties of the callosities relieve or distribute pressure on soft tissues during long bouts of sitting, while their relative immobility prevents slipping on tree branches (M. Rose, 1974). Rose (1974) also pointed out that ground-dwelling cercopithecids utilize their callosities in "shuffling" locomotion, assumed while feeding in crouched postures.

The conformation of the caudal surface of the ischium in *Plesiorhycteropus* is similar to that of cercopithecines in that it is planar and free of muscle scars (which are instead located at the periphery of the expansion). Obviously, cercopithecines lack any sacral, ilial, or vertebral modifications for carapace support, and in this merely negative sense *Plesiorhycteropus* also agrees with them. Perhaps the strongest contrast between monkeys and bibymalagasy is not in the structure of the ischial expansions per se, but in the size of the tail that passes between them. Cercopithecines vary greatly in tail length, but in none of them is the tail large enough in caliber to interfere with sitting. *Plesiorhycteropus*, however, clearly had a tail with a massive root, and it is probable that, if it did sit, it did not assume postures resembling those taken by Old World monkeys. Lumbar features described in the previous section incidentally affect the plausibility of the sitting hypothesis in that more terrestrial cercopithecoid monkeys appear to have a tendency to progressively reduce the width of the neural arch. However, there is no clear pattern among cercopithecids with respect to zygapophyseal separation. Although the correlation of pelvic and lumbar adaptations is indicative rather than dispositive, provision of platforms for sitting pads seems a more likely interpretation of the function of ischial expansions in bibymalagasy than does carapace support.

OTHER CORRELATES

Although both Lamberton (1946) and Patterson (1975) considered *Plesiorhycteropus* to be primarily a digger, Lamberton believed

that bibymalagasy may have been capable of climbing, and Patterson suggested that they may have been able to jump as well.

We may deal first with Patterson's argument that bibymalagasy were capable of jumping. He argued that the long greater trochanter would tend to increase the ability of the gluteus medius to extend the thigh rapidly, and that rectus femoris enlargement—as indicated by the size of its pelvic origin—would assist in this (?by increasing the power of flexion at the hip as well as extension of the leg). He quoted some anecdotal material regarding the utilization of jumping by *Dasyopus*, which also has a long greater trochanter, to ward off predators or to make quick dashes to safety. However, it is clear that the usual mode of progress of the armadillo does not involve leaping, and the analogy as a whole is unsatisfactory. In armadillos, the gluteal musculature probably acts principally to brace the trunk during digging, with the hindlimb in a fixed position. In *Thomomys*, another highly fossorial animal (J. E. Hill, 1937), the greater trochanter is almost as large and projecting as it is in *Dasyopus*. In any case, jumping as a frequent mode of progression in *Plesiorhycteropus* is contraindicated by its hindlimb/intralimb proportions (table 13), and Patterson's idea does not warrant further discussion.

The climbing argument deserves more scrutiny, since there are good examples of digging mammals that are also able arboralists (e.g., smaller manids and vermilin-guans). Lamberton's (1946) stated case for some climbing ability in *Plesiorhycteropus* consists exclusively of the observations that (1) the size of the deltopectoral eminence indicates strong ability to adduct the arms, and (2) the compression of the unguals implies the existence of strong, sharp claws that could have functioned in either climbing or digging. Patterson (1975) cited a larger set of features that seems to support Lamberton's thesis: (1) jumping ability (noted above); (2) humerus similar in shape to that of arboreal phalangiers (as well as *Dasyopus*); and (3) mobile cruro-tarsal and tarso-navicular articulations, permitting motions other than hingelike ones. The narrowness of the distal end of the ulna, while perhaps not a specific adaptation for climbing, is not inconsistent with it, nor is

the presence of tibiofibular fusion necessarily a bar to arboreal activity. All in all, Patterson (1975: 225) concluded, *Plesiorycteropus* may have been "the most versatile of the aardvarks."

As Simpson (1931) observed, osteological differences between arborealists and diggers are not necessarily as sharp as one might conclude on the basis of habitus. Any animal engaged in climbing has to use a method that permits it to both overcome gravity and stay in place on the support (Cartmill, 1985). The use of claws is one such method, and the climbing mammals that rely on claws in this way generally have sharper, more recurved claws than do their terrestrial relatives. *Plesiorycteropus* cannot be directly assessed on this point, although its unguals, if correctly attributed, clearly differ from the blunter, shovel-shaped unguals of *Orycteropus*. The fact that the head of the humerus rises above the tuberosities in bibymalagasy is interesting, because this morphology facilitates raising the arms to or above shoulder height and is therefore a common characteristic of climbers (but see remarks under Correlates of Digging). The enlarged olecranon and the size of the processes on the margins of the sigmoid notch seem at cross purposes with increased range of motion at the shoulder, since they would have limited the amount of extension possible at the elbow. On the other hand, with the trunk erect this set of adaptations would seem well-suited for forcibly raising the body by digging the claws of the partly pronated manus into a vertically oriented substrate such as a tree trunk. In a much larger animal, these adaptations might be plausibly interpreted in reverse, i.e., that they would have facilitated the bringing down of branches, presumably for feeding purposes (cf. "bipedal browsing"; Coombs, 1983). In any case, the reduction of ulnocarpal contact in *Plesiorycteropus*, otherwise so difficult to explain in a committed digger, might be considered a correlate of climbing, in that similar reduction is seen in cautious, nonacrobatic tree dwellers (Cartmill, 1985). The knee joint and the shape of the crurotarsal articulation do not seem to be designed to facilitate tree climbing in any obvious way, but the roughly similar organization found in *Dendrohyrax* (as well as terrestrial hyraxes) demonstrates that this

morphology is permissive rather than restrictive (see also Rasmussen et al., 1990). The hemispherical medial malleolus and astragalar cotylar fossa of *Plesiorycteropus* are also reminiscent of similar complexes in some arboreal primates, such as lemurs ("articular cup" of Lewis, 1989). The substantial bony buttressing of the cranial side of the acetabulum is found in vertically climbing primates, where it presumably acts to resist joint loading at the hip during active arboreal maneuvering. *Plesiorycteropus* was certainly not built for speed, and, in view of its comparative heaviness for an animal of its size, perhaps the correlation is simply with vertical posture—or, again, with the support of some unknown form of armoring.

The digital rays of some climbing mammals are elongated compared to those of their terrestrial relatives (Cartmill, 1985), but the evidence for digital length in *Plesiorycteropus* is inconclusive. For example, whether known metapodials should be considered to be short or long partly depends on which limb they are assigned to. The longest element, a putative "MC" 2 (MNHNP 1657), is 41% of "average" maximum length of the humerus, but only 26% of femur length. If MNHNP 1657 is indeed from the pes, its femoro-metatarsal index would have to be considered low even for a noncursorial ungulate (cf. Williamson and Lucas, 1992) and suggests a comparatively short foot. If it represents the manus instead, one's conclusion would be nearly the opposite, that its humero-metacarpal index is quite comparable to that of digitigrade *Meniscotherium* (Williamson and Lucas, 1992).

On the whole, then, there appears to be some merit to the argument that the limb morphology of *Plesiorycteropus* indicates that it had some climbing ability, or at least was not a strictly terrestrial quadruped. If *Plesiorycteropus* did climb, it must have done so very carefully, in view of its relatively large body mass and tiny eyes. If it went to the trees, it presumably did so to forage. Its best behavioral analogs may be microphthalmic gymnures and shrew tenrecs, some of which are scansorial. These lipotyphlans presumably rely exclusively on olfactory and auditory information when maneuvering in arboreal milieux.

CORRELATES OF DIET AND FOOD PROCUREMENT

Because no parts of the bibymalagasy face or jaws have been recovered (or recognized as such), dietary inferences for *Plesiorhycteropus* must remain speculative. The prevailing view, developed at some length by Patterson (1975), is that *Plesiorhycteropus* was so highly committed to myrmecophagy that it sacrificed both its dentition and a normal jaw articulation. This inference permitted Patterson to go on to argue that *Plesiorhycteropus*—despite strong morphological departures from other aardvarks—could nevertheless be seen as a logical evolutionary development from the more primitive tubulidentate model exemplified by *Orycteropus*.

In order to appraise Patterson's argument that *Plesiorhycteropus* was a definite myrmecophage, it is first useful to determine which traits of extant myrmecophages demonstrably occur in *Plesiorhycteropus*. Morphological features strongly correlated with myrmecophagy have been summarized by several authors (most recently by Smith and Redford, 1990) and are as follows: (1) vermiform tongue; (2) enlarged salivary glands; (3) highly developed olfactory sense, with complex nasal turbinal system; (4) stomach with muscular pyloric area; (5) forearms adapted for digging; (6) reduction in tooth size and cusp complexity; (7) loss of teeth or increase in variability of tooth number; (8) decrease in size and complexity of masticatory muscles; (9) reduction of temporal fossa, postorbital process, and sometimes the zygomatic arch; (10) modification of lower jaw (rodlike structure, reduced ascending portion); (11) glenoid articulation at level of palate; (12) elongated snout; (13) posterior extension of the palate and midline palatal ridge for use in crushing prey (see also Griffiths, 1978; Redford, 1987).

Like all such lists, this one has its limitations. Ants and termites predominate in the diets of *Myrmecobius* and *Proteles*, but these mammals lack many of the myrmecophagous specializations just noted. By contrast, *Dasyus novemcinctus*, which is overwhelmingly "myrmecophagous" according to standard morphological criteria, is in fact a general feeder according to behavioral evidence (Smith and Redford, 1990). More to the immediate point, traits that may be regarded as

uniquely diagnostic of myrmecophagy, such as the long vermiform tongue and hypertrophied pyloric area, are soft-tissue features that cannot be observed in fossils.

Turning now to *Plesiorhycteropus*, we find good grounds for inferring the structural or physiological correlates of traits 3, 5, and 11 in this list, whereas the presence of 8, 9, and 12 is less certain. Traits 1, 2, 4, 6, 7, 10, and 13 either are not preserved in the available hypodigm or have no known osteological correlates. Although the palate is not preserved, all plausible reconstructions of its probable position indicate that it would have been nearly coplanar with the mandibular fossa. The evidence for reduction in masticatory musculature rests largely on the low position of the temporal lines. The direct evidence for associated reductions in the temporal fossa and zygomatic arch is ambiguous. *Plesiorhycteropus* seems to have had a snout of only moderate size, but since this is also true of *Manis* and numbats, the trait may be regarded as having low indicative value. Although the evidence is negative, it is surely pertinent that, despite more than a century of paleontological work in Madagascar, not a single tooth or jaw attributable to *Plesiorhycteropus* has been identified. The only reasonable interpretation consistent with these facts is that bibymalagasy must have expressed, in some unknown but apparently emphatic way, the morphological reductions embodied in traits 6, 7, and 10.

Although the limited evidence is basically consistent with myrmecophagy, it is also true that all it really shows is that *Plesiorhycteropus* had to have ingested food items of soft texture. These items could have been animal, plant, or both. Some mammals that eat significant amounts of ants or termites also eat significant amounts of other things (Redford, 1987), and it therefore seems somehow misrepresentative to pigeonhole them as "myrmecophages." In this connection it is interesting to note that some specimens of the Eocene Messel eutherian *Eomanis waldi*—demonstrably a myrmecophage according to the criteria listed above—have yielded preserved stomach contents that consist mainly of plant remains and only a few insect parts (Koenigswald et al., 1981). The absence of significant quantities of insects is difficult to explain, although Koenigswald et al. (1981)

suggested, somewhat counterintuitively, that chitinous body parts might have been selectively decomposed by formic acid excreted by ingested ants.

If *Plesiorycteropus* was indeed a myrmecophage, its rather small size suggests that it probably did not forage for social insects occupying hardened structures like the mounds constructed by some termite species. It is more likely that its prey would have consisted of larvae or adults opportunistically encountered while the animal was tearing apart nests, stripping off bark, or digging in loose soil. If bibymalagasy were also capable of climbing, they may have predominantly searched in trees, as do the more arboreal species of mandids (Kingdon, 1974).

EXTINCTION OF *PLESIORYCTEROPUS*

When *Plesiorycteropus* became extinct is not known with certainty, although it was presumably before the arrival of Europeans because nothing remotely like it figures in early chronicles (e.g., Flacourt, 1658; Dubois, 1674). For convenience, its final disappearance may be set at ca. 1000 yr BP, the tentative consensus date for the termination of the subfossil extinction event in Madagascar (Dewar, 1984; MacPhee and Burney, 1991). How *Plesiorycteropus* was driven to extinction is understood even less, although this point can be made with equal merit for all of the subfossil taxa (MacPhee, 1986; Burney et al., in press). The starkest evidence for drastic changes in conditions on the island comes from the distribution and contents of subfossil localities. The majority of these localities are situated in places that are now treeless, depauperate savannas, yet they contain—often in extraordinary abundance—the remains of vertebrates that were clearly adapted to arboreal or forest conditions (MacPhee, 1986). In an earlier section (Materials, Tax-

onomy, and Occurrence) it was argued that, in the interior of the island, the terrestrial vertebrate fauna was probably largely restricted to narrow forest belts associated with wetlands. If early human residents of the island burned or otherwise interrupted these narrow corridors (for an analysis, see Burney, 1986), extinctions might have been precipitated quickly because there would have been literally no place for the fauna to escape to (MacPhee, 1986; MacPhee and Raholimavo, 1988).

In Madagascar, most of the disappeared seem to have been herbivores, and almost all of them were large (or could be so considered within the context of their respective phylogenetic groupings). In many late Quaternary contexts (Martin, 1984), large herbivores tended to be at high risk, and in this sense the Malagasy extinction event conforms to patterns seen elsewhere. However, the disappearance of *Plesiorycteropus* may be considered somewhat anomalous in other respects. Bibymalagasy were the smallest non-primate mammals—and the only ones conventionally interpreted as completely insectivorous—to die out in the Malagasy Holocene. ("*Cryptogale australis*" [G. Grandidier, 1928], still sometimes cited as an extinct Malagasy tenrecoid, is indistinguishable from extant *Geogale aurita* [Heim de Balsac, 1972]). That a completely insectivorous mammal would become extinct as a result of loss or reduction in its food supply seems highly improbable, unless, of course, *Plesiorycteropus* was dependent on invertebrates whose distribution was catastrophically affected by forest loss. Yet animals arguably more specialized in diet than was *Plesiorycteropus* (e.g., the predominantly lumbricivorous *Eupleres* [Albignac, 1973] and the opportunistic larvivore *Daubentonina* [Iwano and Iwakawa, 1988]) have managed to survive in Madagascar, despite 20 centuries of human impact on the environment.

We'll teach him to know Turtles from Jays.

— William Shakespeare
Merry Wives of Windsor

The objection, that Tubulidentata and Pholidota each contain only a single genus, is irrelevant so long as our systematics is guided not by numbers but by degree of relationship.

— Max Weber (1928, vol. 2, p. 171 [trans.]),
commenting on the paraphyly of *Edentata
and the erection of separate orders for aard-
varks and pangolins

THE SYSTEMATIC POSITION OF *PLESIORYCTEROPUS*

One does not expect that an ordinal-level placement for an extinct eutherian mammal of late Quaternary age, represented by moderately good skeletal material, would entail much difficulty. But such is the case with *Plesiorhycteropus*. The difficulty is not due to a dearth of recognizably apomorphic features: as preceding sections illustrate, *Plesiorhycteropus* was not a pervasively primitive animal. Rather, as this section illustrates, the problem is to determine which of its apparently derived features actually document its true affinities, because its morphology does not unambiguously align it with any single, monophyletic eutherian group.

Two separate parsimony analyses are presented in this section. The first (Analytical Results Using the 30- and 32-Character Matrices) derives from the present study. The second (Analytical Results Using Novacek's 88-Character Matrix) employs a data matrix originally published by Novacek and co-workers (hereafter, the "88CM"). Although on first impression the two matrices would appear to be quite different, only a small number of the transformations in Novacek's 88CM can actually be assessed in *Plesiorhycteropus*, and most of those are represented in my 30CM. Where they plainly differ is in their respective taxon lists, and the point of interest is to see how the two matrices perform with respect to the placement of *Plesiorhycteropus*.

The polarities and character state assignments made in Novacek's 88CM are largely followed here, although changes are made in certain runs for the purpose of illustrating

how outcomes are affected. The transformation series adopted for the present study are defined and defended in the next section.

CHARACTERS AND TRANSFORMATIONS

Table 18 is a data matrix which compares states of 32 characters among 16 taxa (including a hypothetical Outgroup). In subsequent sections, this is the basic data set used with the program Phylogenetic Analysis Using Parsimony (PAUP, version 3.0s; Swoford, 1989) to search for most-parsimonious arrangements of taxa (see Analytical Results Using the 30- and 32-Character Matrices). The most explicit of the hypotheses to be evaluated is that *Plesiorhycteropus* and *Orycteropodidae* are sister taxa. Less explicit hypotheses are that *Plesiorhycteropus* is more closely related to *Manidae* or, more vaguely, to *Edentata. All of the taxa in the foregoing groups are therefore included in the data matrix. For reasons presented in the Introduction, comparisons are also made to lipotyphlans, hyracoids, and certain taxa included in the traditional concept of *Condylarthra. However, there being no satisfactory reason to believe that these taxa are adequate as outgroups, conditions in other eutherians are frequently referenced in the course of making character polarity decisions.

Characters and states are defined below, together with information on distribution, inferred polarity, and morphological points not discussed in the descriptive sections. The first 30 characters are assessed from direct evi-

TABLE 18
Data Matrix^a

	Outgroup	<i>Plesiorhycteropus</i>	Orycteropodidae	Manidae	Dasypodidae	Myrmecophagidae	Bradypodidae	Megalonychidae	Soricomorpha	Erinaceomorpha	Hyracoidea	<i>Hyopsodus</i>	<i>Ectoconus</i>	<i>Phenacodus</i>	<i>Pleuraspidothierium</i>	<i>Meniscotherium</i>
1. OPTC CANAL	0	1	0	0	0	0	0	0	1	1	0	?	?	0	?	0
2. INTPARIETL	0	0	0	0	1	1	1	1	0	0	0	?	?	?	?	?
3. ALISPH-PAR	0	0	0	1	1	0	0	1	0	0	0	?	?	0	?	0
4. LACRML FAC	0	0	0	1	0	0	1	1	1	1	1	0	0	0	0	0
5. LACRML FOR	0	1	0	?	0	0	0	0	0	0	1	1	1	1	1	1
6. NASL EXPAN	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
7. FOR ROTUND	0	1	0	0	0	1	1	1	0	0	1	0	?	0	0	1
8. FRON-PAR P	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0
9. PTERTY TYMP	0	0	1	0	1	1	1	1	0,1	1	0	0	0	0	0	0
10. CAUD PR PET	0	0	1	0	0,1	0	0	0	0	0	0	0	?	0	0	1
11. TEGMN SIZE	0	1	0	0	1	0	0	0	0	1	1	0	?	0	?	1
12. MAST EXPOS	0	0	0	1	0,1	1	1	1	0	0	1	0	?	0	0	0
13. PERCRN CAN	0	0	0	1	0	0	0	0	1	1	1	1	1	1	1	1
14. EPITYMP SIN	0	0	1	1	0,1	0	1	1	0	0	1	0	?	1	?	1
15. SUBARC FOS	0	1	1	1	1	0,1	1	1	0	0	1	0	?	0	?	0
16. FOR STAPED	0	1	0	2	2	2	2	2	0	1	2	2	?	0	1	0
17. INT CAR POS	0	0	0	1	1	0	1	1	0	0	2	0	?	?	0	0
18. XENARTHRY	0	0	0	0	1	1	1	1	0	0	0	0	0	0	?	0
19. TRNARC CAN	0	1	1	0	0	0	0	0	1	0	0	0	0	0	?	0
20. HUMRL HED	0	1	0	1	0	1	2	2	0	0	0	0	0	0	?	0
21. RAD ULN PR	0	1	0	1	0	0	1	1	1	0	0	0	0	0	?	0
22. PUBIC SYMP	0	1	0	1	1	1	1	1	1	1	0	0	0	0	?	0
23. SACROISCH F	0	0	0	0	1	1	1	1	0	0	0	0	0	0	?	0
24. ISCH LAT PR	0	1	1	0	0	0	0	0	0	0	0	0	0	0	?	0
25. ISCH EXPAN	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
26. LESS TROCH	0	1	0	0	0	0	0	0	0	0	1	0	1	1	?	1
27. FEMUR HED	0	1	1	2	1	0	2	2	0	0	1	0	0	1	?	1
28. ASTRAG CTY	0	1	0,1	0	0	0	0	0	0	0	1	0	0	0	?	1
29. ASTRAG PMP	0	1	0,1	0	0	0	0	0	0	0	0	0	1	0	?	1
30. UNGL PHAL	0	0	1	0	0	0	0	0	0	0	1	0	1	1	?	1
*31. MAN REDUC	0	1	0	1	0	1	0	0	0	0	0	0	0	0	?	0
*32. ZYGO ARCH	0	1	0	1	0	1	1	1	0,1	0	0	0	0	0	?	0

^a Characters 31 and 32 (asterisks) are Patterson characters. See text.

dence in the available hypodigm (hereafter, this group of characters will be referred to as the "30CM"). The remaining two characters frame Patterson's (1975) inferences that the skull of *Plesiorhycteropus* probably lacked teeth and probably had an interrupted zygomatic arch. For reasons discussed elsewhere, there is no direct evidence (as yet) for the existence of these features in *Plesiorhycteropus*, but they are added to the matrix in some PAUP runs

(thus creating a second matrix, hereafter the "32CM") to illustrate their effect on tree construction. No differential weighting scheme was used beyond that inextricably involved in making a selection of characters in the first place. All characters are polarized and multistate characters are unordered. Characters whose states depend on proportions or relative size were quantified where possible.

In view of the amount of descriptive mor-

phology provided in the preceding sections of this monograph, the number of characters selected to support phylogenetic analysis of *Plesiorcyteropus* may be considered rather low by some readers. There are three reasons for the small character base:

(1) Since *Plesiorcyteropus* has no settled place within Eutheria, outgroup comparisons have to be conducted at the level of "other Mammalia." Unfortunately, there are few well-tested osteological characters usable at this level of outgroup comparison (cf. Novacek, 1992a).

(2) The characters selected for use are ones whose polarity I felt could be justifiably determined on the basis of excellent distributional or other relevant evidence—and there just aren't many characters for which the evidence is that good. Characters in the literature with poor (or, worse, unverifiable) distributional information were omitted (see Rejected Characters), as were certain characters, otherwise interesting, whose status could not be ascertained in *Plesiorcyteropus*. It would have been possible to extend the size of the data matrix by including characters whose polarity was ambiguous, that is, whose ancestral condition could not be reasonably determined through outgroup comparisons. Frost et al. (1991) used several unpolarized characters in their phylogenetic assessment of Erinaceidae, on the ground that such characters do not affect the rooting of the most parsimonious tree(s) (hereafter, MPTs), but do potentially serve to enhance stem definition. In such an approach, the polarity of transformation of unpolarized characters is determined by their correlation with remaining (polarized) characters. This approach amounts to a covert form of weighting since it is the remaining, polarized characters that will determine the topology. I maintain that this option is unworkable with data sets as noisy as the present one.

(3) Many of the most interesting skeletal features seen in *Plesiorcyteropus* are autapomorphies, valuable for constructing diagnoses but collateral to the identification of monophyletic groups. While such characters could be added to the data matrix, PAUP will simply force them onto terminal branches.

It will also be noted that in the 30CM there is a rough 3:2 ratio of cranial (17) to post-

cranial (13) characters. Some of the most derived features of the bibymalagasy skeleton are to be found in the postcranium, and I wanted to ensure that they received adequate consideration by including them in the analysis. This was necessary in any case, because the skull is incompletely known in *Plesiorcyteropus* and what we have of it is not particularly helpful for assessment of affinity.

The morphological diversity of Tubulidentata is extremely low; for the characters considered here, *Leptorycteropus* and *Myorycteropus* are so like modern *Orycteropus* that they give no perspective on character phylogeny within this undoubtedly ancient group. Accordingly, Tubulidentata is represented by only one terminal taxon (*Orycteropodidae*) in the data matrix.

Patriomanis differs from extant pholidotans in many details of skeletal anatomy (Emry, 1970), usually in the retention of apparent eutherian plesiomorphies. For observable states of the characters considered here, however, no differences of note were manifested except in the case of character 23 (q.v.). For this character, the state in *Patriomanis* was used to polarize the symplesiomorphous state for the family.

The trouble with condylarthran taxa is that, in the absence of an acceptable phylogenetic hypothesis for their relationships (but see Thewissen and Domning, 1992), each taxon has to be entered into the analysis separately. Character states for included taxa are uncertain in a number of instances (table 18), which amplifies tree instability.

Several primary sources in the literature were frequently consulted for characters. Any osteological character found therein that could be evaluated on the basis of the *Plesiorcyteropus* hypodigm was carefully scrutinized for accuracy; if it survived this process, it was added to the total. Some authors and characters are denoted by a letter-number combination, as follows: N, Novacek (1986, sequence number from his table 3); NWM, Novacek and co-workers (Novacek and Wyss, 1986a; Novacek et al., 1988; Novacek, 1989; Novacek, 1992a; sequence number from table 2 in Novacek et al., 1988); PMF, Prothero and co-workers (Prothero et al., 1988, sequence number from their table 8.1); E, Engelmann (1978, sequence number from his running total). It should be noted that char-

acter definitions, and often distributions and polarities as well, are sometimes different from the ones given by referenced authors. Differences that are noted but not discussed can be checked by examining specimens.

1. Optic canal: (0) unreduced (index > 0.4); (1) reduced (index < 0.3)

Morphological Discussion: See Morphology of the Cranium: Foramina of Orbit.

Polarity Validation: One of the outstanding features of the skull of *Plesiorhycteropus* is the tiny size of the optic canal (Thewissen, 1985). Novacek (1986: 30) considered a "moderately large" optic canal like that of *Leptictis* to be primitive for eutherians, but offered no means of judging size in a consistent, quantitative manner. One possibly meaningful way would be to compare optic canal size to a measure of brain size, but in the absence of good data for most groups I have not undertaken this comparison. I have instead compared the sizes of the optic canal and the infraorbital foramen in order to derive an optic canal index. There is some biological justification for this approach. Highly macromammalian animals tend to have small eyes and a very large general sensory input from cranial nerve V2; their indices will therefore be low. Those more dependent on vision typically have a smaller V2 input (and therefore a smaller infraorbital foramen); their indices will be higher. It is recognized that infraorbital arteries and veins generally pass through the same aperture as the infraorbital nerve, and that therefore the caliber of the nerve must be less than that of the foramen. However, all of the apertures to which the optic canal might be usefully compared suffer from similar complications.

I measured the shortest diameters of the optic canal and infraorbital foramen in representatives of a selection of taxa using a microscope equipped with a measuring reticule. The only difficulties experienced revolved around the appropriate orientation of skulls in which the flaring margin of the sphenorbital fissure partly concealed the optic foramen (e.g., as in *Tenrec*), or in which the zygomatic arch interfered with a direct view of the optic canal. These problems were overcome by manipulating specimens until reasonably unimpeded views of canals could be achieved. It is not felt that these orientation

problems seriously affected the accuracy of measurement. Specimens with multiple (or subdivided) infraorbital foramina were not measured. I then computed "optic canal size" indices for these data, dividing the vertical diameter of the optic canal by the shortest diameter of the infraorbital foramen. Indices for lipotyphlans were consistently low (range, taxa with functional eyes: 0.1 [*Solenodon paradoxus*] to 0.3 [*Hylomys suillus*]). *Orycteropus* was somewhat higher at 0.5, and *Dendrohyrax dorsalis* was much higher at 0.9. Armadillos were consistently low (range: 0.3 [*Dasypus novemcinctus*] to 0.5 [*Zaedyus chilensis*]), but both genera of living sloths were considerably higher (~1.0), and anteaters had the highest indices in the comparative set (*Tamandua tetradactyla*, 1.4; *Myrmecophaga tridactyla*, 3.3; *Cyclopes didactylus*, 3.5). Manids clustered around 1.0 (with *Manis tetradactyla* highest at 1.2).

Plesiorhycteropus could not be directly rated, since the part of the face bearing the infraorbital foramen is not yet known. However, (1) the diameter of the optic canal (1.0 mm) is consistent with a very small optic nerve, and (2) the diameter of foramen rotundum (5.0 mm in MNHNP 327, right side) is consistent with a very large V2. The maxillary nerve typically receives only a few sensory branches from the nasopharynx, teeth, and gums in the interval between the infraorbital foramen and foramen rotundum. Accordingly, it is reasonable to argue that it changes little in caliber through this distance, and that therefore the proportion of interest lies between 1:4 and 1:5.

Use of a convenient "gap" in continuous data as a device to segregate character states is logically objectionable (see Campbell and Frost, 1993), and I hope that the morphological justifications provided above justify the distinctions made here.

Variation Within Terminal Taxa: Novacek (1986) states that xenarthrans, pholidotans, tubulidentates and hyracoids display his primitive character state. In view of the optic canal indices for these groups, it is clear that *Plesiorhycteropus* had a derivedly small optic canal, like that of living insectivores. Dasypodids could have been scored as polymorphic, but they seem to be predominantly at the low end of the 'moderate' category and are so classed here. Extremely small eyes in

terrestrial mammals, as seen in some living lipotyphlans and a few other eutherians (e.g., naked mole rats), appear to be a specialization connected with fossorial life. Obviously, very large eyes (and concomitantly large optic nerves) are derived in another direction, but I have not considered this character state here.

I have no good measurement data for condylarthrans, because in the material available to me the area of the optic canal was either unprepared or crushed. *Phenacodus* is described as having a comparatively small canal (Thewissen, 1990), but it appears to be larger (relative to infraorbital foramen size) than in any lipotyphlan, and is considered primitive here. Williamson and Lucas (1992, p. 6) describe the optic canal as "large" in *Meniscotherium*.

2. Interparietal: (0) present; (1) absent

Morphological Discussion: See Morphology of the Cranium: Cranial Roof and Occipital Region.

Polarity Validation and Variation Within Terminal Taxa: It is possible that we are dealing with a distinction without a difference in the case of this character. In recent years there have been several "new" discoveries of the interparietal in taxa previously said to lack it (cf. Novacek, 1993a), and it seems abundantly clear that without ontogenetic data no certainty about presence/absence is warranted. The only justification I have for using it in this analysis is that, absent definitive evidence to the contrary, its loss may be a xenarthran synapomorphy. Hyracoids have an interparietal, but its distribution among other ungulate orders is controversial. It has not been identified in any condylarthran, but this is practically meaningless as observational evidence given this element's tendency in many extant groups to fuse early in ontogeny to the parietals and supraoccipital.

3. Alisphenoid, temporal wing: (0) dorsally extensive, in broad contact with parietal; (1) ventrally confined in orbital wall, not in broad contact dorsally with parietal (NMW 27)

Morphological Discussion: See Morphology of the Cranium: Orbital Mosaic.

Polarity Validation and Variation Within Terminal Taxa: This character has been the subject of a recent investigation by Rose and Emry (1993), and it is clear from their dis-

cussion that variation in terminal taxa is greater than has been assumed in the past. The basic difficulty here is that in defining characters of the orbital mosaic, one has to simultaneously evaluate several suture lines and bone territories, each of which can vary independently of every other. This is clearly a character whose evaluation would benefit from an ontogenetic study of patterning.

The widely accepted primitive state is represented in *Orycteropus* (including *O. afer* and *gaudryi*), in which the alisphenoid is dorsally extensive and meets the parietal along a broad front. In this taxon the parieto-alisphenoid suture is a simple approximation of bone territories, i.e., the parietal does not overgrow other elements in order to meet the alisphenoid (cf. Parker, 1885). Conditions in lipotyphlans are often hard to rate because sutures are usually obliterated in adults. However, I find that *Solenodon paradoxus*—which descriptively possesses broad parieto-alisphenoid contact in late stages—achieves this character state only because a tongue of the parietal overgrows the rear of the frontal bone (cf. AMNHM 28272, a young juvenile). In the absence of overgrowth by the squamous part of the parietal, it seems likely that there would have been fronto-squamosal contact. In *Erinaceus europaeus* there are also overlaps, but in this case the alisphenoid is intracranially even more dorsally extensive than it appears to be extracranially, lapping broadly onto the frontal as well as the parietal (cf. Parker, 1885). In noncingulate xenarthrans and also in manids, the alisphenoid is not as dorsally extensive, largely because of frontal expansion. However, there is more than one pattern of sutural contact. Recent sloths differ from each other: *Choloepus* lacks parieto-alisphenoid contact but *Bradypus* possesses it (cf. Rose and Emry, 1993). Armadillos are also variable: the stellate pattern (in which the alisphenoid, parietal, frontal, and squamosal form a four-way junction), described as general for armadillos by Novacek and Wyss (1986a), is uniformly typical only of *Tolypeutes matacus* (Rose and Emry, 1993) and otherwise frequent only in *Dasybus novemcinctus* (personal obs.). In other Dasypodidae, Rose and Emry (1993) observed (and I affirm) that the alisphenoid and the parietal are separated by broad fronto-squamosal contact (as in *Manis*). On the basis

of its distribution I take this latter conformation to be primitive for that family. In myrmecophagids there is an autapomorphously large orbital wing of the parietal, which in most anteaters extends so far rostroventrally that wide parieto-alisphenoid contact is achieved despite the fact that the alisphenoid itself is small. The exception is *Cyclopes*, in which a stellate pattern is typical (see also Rose and Emry, 1993).

Alisphenoid-parietal contact is illustrated for *Phenacodus intermedius* by Thewissen (1990) and for *Meniscotherium chamense* by Williamson and Lucas (1992), but I am not able to discern the precise composition of the orbital mosaic in other condylarthrans.

As noted in the descriptive section, the available bibymalagasy skulls notably differ for this character. MNHNP 327 is rather like *Tolypeutes matacus* in having a stellate arrangement of bone territories, at least on one side. MNHNP 328, however, displays broad fronto-squamosal contact, much like that seen in pholidotans and the majority of armadillos. USNMP 407080, by still further contrast, has significant alisphenoid-parietal contact and thus no fronto-squamosal articulation. My solution is to pay attention to the fact that, whatever the fine details of mosaic arrangement, the alisphenoid's orbital wing is dorsally extensive in all specimens. This constitutes a notable resemblance to *Orycteropus* and other eutherians thought to have a primitive arrangement of orbital elements, and *Plesiorycteropus* is scored accordingly.

4. Lacrimal: (0) with facial process; (1) confined to orbit and orbital rim, lacking a facial process (NMW 85)

Morphological Discussion: See Morphology of the Cranium: Facial Region.

Polarity Validation and Variation Within Terminal Taxa: Distributional information assembled by Novacek (1986) tends to indicate that a moderately extensive facial wing of the lacrimal is primitive, although the evidence is far from uniform. If a large lacrimal facial process is plesiomorphous, lipotyphlans are derived relative to the eutherian morphotype in having the lacrimal ending at or near the orbital rim. This appears also to be true of hyraxes, although in Oligocene *Geniohyus* the lacrimal was somewhat more facially extensive (Dechaseaux, 1958). A large

wing is assumed to be primitive for xenarthrans because of the broad distribution of this character state within the group, but the Recent taxa provide no clear signal. The facial wing can be described as consistently large only in dasypodids; in both kinds of sloths it is always small. Myrmecophagids vary; the wing is very large in *Myrmecophaga*, smaller in *Tamandua*, and negligible in *Cyclopes* (which I take to be secondary). The lacrimal is tiny in manid species that retain this element (Weber, 1928; Patterson, 1978). Manids could be treated as polymorphic for this trait if an additional derived state (absence) were specified, but there was no purpose in doing so here.

Although the lacrimal is not complete in the available specimens of *Plesiorycteropus*, enough remains to establish beyond doubt that it possessed an extensive facial wing, as does *Orycteropus*. In *Hyopsodus*, *Ectoconus*, *Phenacodus*, *Meniscotherium*, and evidently *Pleurospirotherium* the facial wing may be counted as large, although its most extensive portion is directed upward rather than forward (unlike the condition in *Orycteropus*).

5. Lacrimal foramen, position: (0) opens laterally on antorbital rim or facial wing of lacrimal; (1) opens posterolaterally within orbit (N 23)

Morphological Discussion: See Morphology of the Cranium: Facial Region.

Polarity Validation: This is a character whose polarity will probably never be generally agreed upon by morphologists and systematists, partly because the position of the foramen with respect to the antorbital rim is often ambiguous in mammals lacking sharply defined orbits. Thewissen (1985), defining a similar character in his study, concluded that the intraorbital position is primitive for eutherians, apparently on the basis of fossil evidence. However, distributional evidence for extant taxa indicates that the extraorbital position (as I understand it) is much more frequent and I have therefore sided with Novacek (1986) in considering this the primitive state.

Variation Within Terminal Taxa: No significant variation was encountered within terminal taxa. I have accepted Starck's (1967: 505) authority in holding that the lacrimal foramen is completely missing in all pholi-

dotans and therefore have rated Manidae as uncertain as to character state. However, I note that on the discrete lacrimal of *Manis tetradactyla* there is sometimes a pinhole, of uncertain homology but in the position expected for a lacrimal foramen, which perforates the tiny facial wing (fig. 6). Lacrimal foramen location in condylarthran genera is based on the authority of Matthew (1937), Gazin (1965, 1968), Thewissen (1990), and Williamson and Lucas (1992).

6. Nasals, rostralateral margins: (0) parallel or slightly divergent; (1) widely divergent rostrally

Morphological Discussion: See Morphology of the Cranium: Facial Region.

Polarity Validation and Variation Within Terminal Taxa: Marked expansion of the rostral ends of the nasals, at least to the degree seen in *Plesiorcyteropus*, is extremely rare in extant mammals (among the few examples encountered: *Phoca*, *Zalophus*, *Geomys*, *Babryrousa*).

In Dasypodidae there is a familywide tendency for slight rostral expansion (cf. Engelmann, 1978). Particularly striking is the correspondence between the bibymalagasy condition and the comparatively short and rostrally very broad nasals of *Holmesina septentrionalis* (cf. AMNHP 45773), an extinct cingulate possibly phylogenetically closer to glyptodonts than to true armadillos (Engelmann, 1985). Other conditions seen in extant members of the comparative set are not at all comparable. (*Cyclopes didactylus*, but no other anteater, has an hourglass configuration in which the central portions of the nasals are constricted and both ends are broadened; I consider this to be an autapomorphy of silky anteaters.)

7. Foramen rotundum: (0) confluent with spheno-orbital fissure; (1) separate from spheno-orbital fissure

Morphological Discussion: See Morphology of the Cranium: Foramina of Orbit.

Polarity Validation and Variation Within Terminal Taxa: According to Novacek (1986), distributional evidence implies that a separate aperture for V2 is derived (contra Engelmann, 1978), this condition being common only in xenarthrans, scandentians, euprimates, and pholidotans. However, there are a number of exceptions within these

groups (Zeller, 1989), and a separate foramen occurs sporadically elsewhere in Eutheria. In Xenarthra, the foramen rotundum is common only in sloths and myrmecophagids (rare in *Tamandua*; for variation, see Wetzel [1985]). Among armadillos, I found a separate foramen rotundum only in occasional specimens of *Tolypeutes* (e.g., AMNHM 248394, right side only). My sense of foramen incidence in pholidotans is that it is almost always absent (contra Novacek, 1986), and this is reflected in the scoring of this character.

There is definitely a separate foramen rotundum in hyraxes (in which it is hidden by a bridge of bone) (Thewissen, 1990). According to Thewissen's (1985) data, this foramen is usually confluent with the spheno-orbital foramen in other ungulates (true of artiodactyls, cetaceans, sirenians, and many others, mostly extinct). There is no separate foramen rotundum in *Hyopsodus* (Gazin, 1968) and one is apparently lacking in *Pleurospirotherium* (Russell, 1964; but see Thewissen, 1985). The foramen rotundum and spheno-orbital foramen were said to be separate in *Meniscotherium* by Gazin (1965), a fact recently confirmed by Thewissen (1985) and Williamson and Lucas (1992). Thewissen (1990) has also determined that there is only a spheno-orbital fissure in *Phenacodus*.

Because all available *Plesiorcyteropus* skulls are severely damaged in the orbital region, it is not in fact certain that the morphology found in MNHNP 327 (i.e., separate foramen rotundum) is typical for the taxon. However, there is sufficient reason to suspect that this is the case and I have therefore assigned the derived character state to bibymalagasy.

8. Frontal/parietal proportions: (0) subequal; (1) frontal elongated relative to parietal

Morphological Discussion: See Morphology of the Cranium: Skull Shape and Proportions.

Polarity Validation and Variation Within Terminal Taxa: Primitively, the parietal forms a larger part of the area of the cranial vault than does the frontal. This is evident in the comparative set among soricomorphs, although it is necessary to examine juvenile specimens with open sutures in order to appreciate this point. In general erinaceomorphs (e.g., *Erinaceus*) are similar, al-

though in some taxa (e.g., *Echinosorex*) the interparietals send a long rostral tongue along the sagittal crest. Measurements taken along this crest (table 7, measurement IV) erroneously imply that the parietals are small relative to the frontal. I have therefore ignored this complication in scoring erinaceomorphs. If it is correct that the large element invading the cranial vault from the rear in the sloth families is the supraoccipital and not the interparietals, then the frontal can be considered to be (marginally) longer than the parietals in bradypodids and megalonychids. It can be seen in figure 6 that frontal elongation is most apparent in pholidotans, dasypodids, and myrmecophagids, while tubulidentates and hyracoids evince the primitive condition. This is pertinent, since it shows that both conditions of the frontal are consistent with rostrum elongation or elaboration of the turbinal system. Condylarthrans in which sutures can be identified also show the primitive condition (cf. Matthew, 1937). (The condylarthrans examined here also evince another primitive trait not scored here, parietals very narrow.) Primitiveness is also clearly present in *Plesiorcyteropus*, despite the fact that the cranial roof is not complete in any single specimen.

9. Pterygoid, contribution to tympanic floor: (0) absent; (1) present

Morphological Discussion: See Morphology of the Cranium: Tympanic Floor.

Polarity Validation and Variation Within Terminal Taxa: In eutherians the body of the pterygoid (with or without a contribution from the basisphenoid) occasionally extends posteriorly, to form a tympanic process that helps to define the anteromedial wall of the tympanic cavity (Van Der Klaauw, 1931; MacPhee et al., 1988). The only group in which pterygoid contribution to the floor could be considered extensive is Xenarthra. In *Choloepus*, the pterygoid (together with the basisphenoid) is markedly inflated and forms an oval blister on the basicranium in front of and medial to the tympanic cavity. In *Bradypus*, the pterygoids form massive—but uninflated—vertical plates, the caudal margins of which briefly contact the bulla and help to define the carotid foramen. Maximum development is seen in myrmecophagids, in which the pterygoids extend far to the

posterior and lap broadly onto the bullae. Manids are similar, except that bullar onlap is less significant. *Myrmecophaga* and *Tamandua* are further modified in that the ventral edges of pterygoids are medially reflected and meet in the midline, thus forming a prolongation of the choanal floor that extends almost to the transverse level of the jugular foramen. *Cyclopes* displays what I take to be a more primitive condition [contra Engelmann, 1978], in which the pterygoids do not meet but form the walls of a long axial channel, as in *Manis*. The pterygoids are also well developed in armadillos compared to most other eutherians, but they are not as enlarged or as inflated as in other xenarthrans. In all dasypodids, the pterygoids extend to the region of the (anterior) carotid foramina, which in almost all species they actually help to define. In *Orycteropus*, the pterygoids are large as well, but with the important difference that they are rostrally directed, and thus have no relationship with the auditory region or the internal carotid. The same is true of hyraxes and condylarthrans. *Meniscotherium terrae-rubrae* AMNH 4447 displays somewhat inflated pterygoids, but they are not caudally extensive (cf. *M. chamense*; Williamson and Lucas, 1992). Pterygoid material contributes to the area bearing the gutter for the auditory tube in erinaceomorphs and in soricomorphs with basisphenoid tympanic processes (MacPhee, 1981).

Although there is no sutural demarcation between basisphenoid and pterygoid in the available specimens of *Plesiorcyteropus*, it is reasonable to assume that the posteriorly projecting eminences in the rostromedial corner of the auditory region are pterygoid by origin. (To provide the proper level of ambiguity, they could be described as tympanic processes of the pterygoid-basisphenoid; trait incidence is exactly the same.)

10. Caudal tympanic process of the petrosal: (0) present; (1) negligible or absent

Morphological Discussion: See Morphology of the Cranium: Tympanic Floor.

Polarity Validation: Distributional evidence strongly indicates that this process is a primitive eutherian (or therian) feature (MacPhee, 1981; Wible, 1990). Therefore its loss or extreme attenuation is frequently counted as derived within Eutheria, although

in practice it is often difficult to compare treatments of character states because morphological criteria for state recognition often vary. My own criteria are set out elsewhere (MacPhee, 1981), although it is admittedly difficult in some situations to transfer recognition criteria from fetal to adult anatomy.

Variation Within Terminal Taxa: Prothero et al. (1988) listed "long" caudal tympanic process of the petrosal as one of the few derived features of ungulates that are also seen in tubulidentates, but their assessment is incorrect. Cifelli (1982: 802), who was their source of information, included *Orycteropus* among mammals in which the tympanic process "is developed ventral to the fenestra rotundum and partially or completely occludes that opening when arching over to the tympanohyal." In fact, the caudal tympanic process of the petrosal is negligible in *Orycteropus*, as Thewissen (1985) noted. Because of fusions it is difficult to determine bullar constitution in adult manids, but in *Manis tetradactyla* AMNHM 53866 it is clear that the ectotympanic is supported on a pedestal of petrosal material, which I take to be the caudal tympanic process (cf. Wible, 1984). The caudal process is identifiable in skulls of young *Cyclopes*, and on this basis I infer that the outgrowth is generally present in myrmecophagids. Dasypodids are variable: a small process is present in *Cabassous*, but I am unable to determine composition in other bullate armadillos. Wible (1984) stated that one can be identified in the fetus of *Dasypus novemcinctus*, but in adults of other taxa with incompletely ossified tympanic floors the process seems to be uniformly absent (e.g., *Priodontes*, *Tolypeutes*).

For the reasons given in the descriptive section, conditions in bibymalagasy are somewhat ambiguous. However, in the best preserved specimen (USNMP 474080), the caudal process is certainly present. Since it partially shields the fenestra cochleae, its morphology probably corresponds to what Prothero et al. (1988) had in mind in describing their derived character state. However, it is useless for the purpose intended (as defined, it does not unite tubulidentates with ungulates), and inspection of the data matrix and other data (e.g., MacPhee, 1981) adequately demonstrates that it is absence, not presence, of the caudal process that is the rare

derived state within Eutheria. It is not possible to determine bullar constitution in adult hyraxes by inspection, but Fischer (1989) has determined from fetal material that a caudal tympanic process of the petrosal exists (heretofore incorrectly identified as a caudal entotympanic; cf. Van Der Klaauw, 1931). I score the process as absent in *Meniscotherium* (cf. fig. 6 of Williamson and Lucas, 1992).

11. Tegmen tympani: (0) small, restricted to zona facialis, forms only a small part of roof; (1) large, expanded to cover epitympanic recess

Morphological Discussion: See Morphology of the Cranium: Tympanic Roof.

Polarity Validation and Variation Within Terminal Taxa: Although apparently always present in eutherians, the tegmen tympani is usually not laterally or rostrally extensive. More often, the roof of the tympanic cavity is covered either by the spheno-obturator membrane, or by squamosal and alisphenoid epitympanic wings, or by both membrane and bone (MacPhee, 1981; Wible and Martin, 1993). I define a "small" tegmen as one that forms no more than a narrow ledge immediately adjacent to foramen faciale (zona facialis). A "large" tegmen is one that spreads out from there, either rostrally or laterally (or both), to form at least half of the roof posterior to the sphenopetrosal epitympanic suture (or, if present, the piriform fenestra).

By this criterion, large tegmina are represented in hyraxes, erinaceomorphs and armadillos among the groups investigated here. In these eutherians, tegmina are long as well as wide, and fill most of the tympanic roof at the expense of the sphenoid and squamosal. (Possession of this character state does not imply absence of the piriform fenestra.) Large tegmina are also present in *Erinaceus* and *Hylomys*, which implies that this feature can be taken as symplesiomorphic for erinaceomorphs. Tegminal enlargement also appears to apply to *Meniscotherium* judging from Gazin's (1965) and Williamson and Lucas' (1992) illustrations (but see also Cifelli, 1982). In manids and nondasypodid xenarthrans, by contrast, tegminal development tends to be weak. Aardvarks possess a negligible tegmen, not unlike that of a sorcid or tenrecid (cf. MacPhee, 1981). *Hyopsodus* and *Phenacodus* seem to be primitive as well (Ci-

felli, 1982; Thewissen, 1990). For *Pleuraspidotherium*, Russell (1964: 257) described a *toit du tympan*, but it is not clear whether the roof in question is exclusively tegmental.

Large tegmina are rarely encountered in groups other than the ones just specified. Novacek's (1989) character 83 is similar in content to this one, but he defined it in such a way that the derived state is limited to primates and scandentians. The tegmen tympani is also extensive in elephant shrews (MacPhee, 1981).

12. Mastoid exposure in ventral basicranium and occipital region: (0) moderate to extensive; (1) reduced or absent (NMW 32, PMF 12)

Morphological Discussion: See Morphology of the Cranium: Tympanic Roof.

Polarity Validation and Variation Within Terminal Taxa: "Mastoid exposure" is poorly defined in the literature. For some authors (including this one), reduced mastoid exposure means that little of the mastoid portion of the petrosal can be seen from *any* angle. For others, however, mastoid exposure is determined from a specific cranial aspect, such as the occipital or basicranial.

Myrmecophagids quickly lose the suture between the squamosal and the mastoid, but I have found its remnant in young specimens of *Cyclopes didactylus* (e.g., AMNHM 98522, 98525). In this species, the suture runs dorsally and somewhat obliquely above the stylomastoid foramen, thereby defining an area of mastoid exposure on the lateral sidewall of the skull. Ventrally, the mastoid is largely covered over by the expanded ectotympanic. On this basis I rate anteaters as derived. Similar conditions obtain in a young *Tamandua tetradactyla* (AMNHM 23563). Young stages of sloths (AMNHM 133429, 5494) are morphologically very similar to anteaters with respect to the degree and location of mastoid exposure. Dasypodids also display a general tendency for the squamosal, alone or in combination with the ectotympanic, to spread over the mastoid region, but in these xenarthrans the morphological picture is more varied. In armadillos with large, inflated bullae (e.g., *Euphractus*, *Chaetophractus*), mastoid exposure is limited to the zone caudal to the foramen for the great diploetic artery. In *Dasypus* the mastoid is exposed more widely in

the triangle above the stylomastoid foramen, while in *Priodontes* and (especially) *Tolypeutes* the mastoid is ventrally, laterally, and occipitally extensive. Because of this, dasypodids must be rated as polymorphic. In manids the mastoid is reduced to no more than a tiny strip located in the region behind the stylomastoid foramen. In hyracoids the squamosal expands ventrally and caudally to such an extent that it enwraps the base of the paroccipital process and forms a sutural junction with the exoccipital. A small portion of the mastoid, marked by a sutural boundary, is sometimes exposed ventrally (cf. figs. 6, 8). All other extant terminal taxa under consideration here display the primitive condition.

There is some confusion evident in the literature concerning the scoring of this character in condylarthrans. Prothero et al. (1988, their table 8.1) indicated that meniscotheres and phenacodonts (among other taxa) derivedly possess "weak" mastoid exposure, but Thewissen and Domning (1992) scored the same groups as primitive (extensive exposure). Thewissen (1990: 82) stated, without comment, that the squamosal "articulates with the mastoid on the occipital aspect of the skull" in *Phenacodus*—the same aspect in which Prothero et al. (1988; see also Fischer and Tassy, 1993) find mastoid exposure to be weak. Russell's (1964: 259) description of *Pleuraspidotherium* implies that the mastoid is actually well exposed in this genus, which does not comport with the scoring of this character for phenacodonts as a group by Prothero et al. (1988). Williamson and Lucas (1992: fig. 4) illustrated a "mastoid process" for *Meniscotherium*, but did not provide a description or an indication of sutural margins. I attempted to check the degree of mastoid exposure in *Ectoconus majusculus* (AMNHP 16500) and *Meniscotherium terraerubrae* (AMNHP 48002), but I found that I could not satisfactorily trace sutural boundaries. With some hesitation, I have accepted Thewissen and Domning's (1992) scoring, but cannot claim to have corroborated it.

Novacek and co-workers distinguished complete amastoidy as an entirely separate character (NMW 60), but I regard this condition to be logically linked to the derived character state defined here. This state is clearly derived relative to the eutherian morphotype, although its distribution suggests

that mastoid reduction has appeared on several occasions.

13. Percranial canal: (0) present; (1) absent

Morphological Discussion: See Morphology of the Cranium: Mastoid Region.

Polarity Validation and Variation Within Terminal Taxa: Identification of the percranial canal should be comparatively simple, but there are three difficulties: (1) its comparative morphology is not well understood; (2) apertures apparently homologous with it can be situated in various positions in different mammalian groups; and (3) because of (1) and (2) it is easily confused with other ports on the rear of the skull—particularly the mastoid foramen. Because the loss of the mastoid foramen has been described by Prothero et al. (1988) as a derived trait uniting all Ungulata, I had hoped to be able to offer a practical comparative anatomy of this and other relevant foramina in the analysis of this character. Unfortunately, it is clear to me that the percranial canal and mastoid foramen are so thoroughly confused in the literature that it will take a major effort to sort them out. For the purpose of this analysis, I will therefore confine myself to brief anatomical diagnoses and character state distributions.

The mastoid foramen can be securely identified by the following criteria: it “pierces the bone above the base of the mastoid process and near, or on, the occipitomastoid suture; it transmits an emissary vein from the sigmoid sinus” (Warwick and Williams, 1973: 266). In eutherians, the foramen (when present) is located at or near the junction of the mastoid, squamosal, and supraoccipital. It is thus always situated on the medial aspect of the otic capsule, and its presence is considered primitive (cf. Novacek, 1986).

The percranial canal is the tube for the great diploetic artery, primitively a “branch of the mammalian stapedia system that connects the posterior branch of the ramus superior and the occipital (or posterior auricular) branch of the external carotid system” (Wible, 1987: 120). “Percranial canal” is offered here as an alternative to “posttemporal foramen,” which has a rather specific connotation in monotreme morphology that is inapplicable here. It is considered primitive to possess this artery and therefore the canal

(Wible, 1987). Generally, the percranial canal is situated more laterally on the sidewall of the skull than the mastoid foramen, but because it usually penetrates the same structure (mastoid region of the temporal), there is occasion for confusion.

Novacek (1986) rated the mastoid foramen as present and large in pholidotans, but in no specimen of any species represented in the AMNH collection is there an aperture in a location that is correct for the true mastoid foramen. (Amastoidy ought not to affect the expression of this trait; although covered externally, the mastoid region of the petrosal in manids is normally positioned inside the endocranium.) There are tiny diploic emissary foramina on the exoccipital, larger ports (probably for rami temporales) on the rear of the parietal, and possibly venous foramina buried in the jugular foramen; none of these, however, corresponds to the mastoid foramen as here defined. Nor is there a percranial canal in the adult, although there is a great diploetic artery, at least in the fetus (Wible, 1984). This artery has been reduced to a terminal branch of the stapedia system that no longer reaches the external carotid system, and seems to involute during later development (Wible, 1987). It appears that manids have substantially reorganized their venous and arterial patterns, and have lost both the mastoid and percranial conduits.

In bradypodids and megalonychids the percranial canal is located high up on the mastoid region, in an alcove posterior to the external acoustic meatus. In myrmecophagids, the canal is said to be relocated to a position between the parietal and squamosal, dorsal to the external acoustic meatus (Wible, 1984). This aperture—more of a foramen than a canal—was found by Wible (1984) in *Tamandua* (cf. fig. 6) and *Myrmecophaga* but not *Cyclopes*. On this basis he inferred that the great diploetic artery either fails to enter the cranial cavity or is completely absent in the silky anteater. A wider sampling of *Cyclopes* skulls indicates that a foramen in the position of the percranial canal is frequently present but always tiny. Finally, there is a small foramen situated more posteriorly than the aperture identified as the percranial canal (identified as *trou mastoïdien* by Guth [1961]) that appears to link up with it. This is too

lateral in position for a mastoid foramen sensu stricto, but is a more typical placement for the percranial canal (cf. fig. 6, *Tamandua*). The vermilinguan condition will be considered equivalent to that of sloths for the purpose of this character analysis, but it is clear that aperture position is not identical.

In armadillos, conditions are complicated by the presence of an additional feature, which I shall simply call the "sulcus for the occipital artery." In extant armadillos, there is always a groove (sometimes a semicanal, less often a complete tube) on the rear of the mastoid region. This sulcus contains the occipital artery (J. Wible, personal commun.). In or at one end of the occipital artery sulcus there is always a canal that leads into the substance of the mastoid. This channel contains the great diploetic artery (J. Wible, personal commun.), and therefore corresponds to the percranial canal.

The tubulidentate case is harder to interpret, because published descriptions of vasculature are inadequate to explain osteological anatomy. In *Orycteropus afer* (and also *O. gaudryi* AMNHP 20694), there is a large foramen penetrating the lateral aspect of the mastoid, near the petrosquamous suture and therefore in essentially the same place as the percranial canal of nonmyrmecophagid xenarthrans. The main difference is that in aardvarks this foramen is not associated with an identifiable groove for the occipital artery. The channel continues into the substance of the petrosal (determined in fetal *O. afer* AMNHM 51395), in which it could not be traced further. Nothing conforming to this channel or its possible contents is identified by Le Gros Clark and Sonntag (1926), du Boulay and Verity (1973), or Thewissen (1985), although the last author noted that there is disagreement among sources as to the place of origin of the occipital artery. Although the evidence is by no means clear for tubulidentates, I tentatively conclude that the channel in question is the percranial canal, that the great diploetic artery is consequently present in aardvarks, and that this vessel probably connects with the ramus superior of the stapediale or its distributaries.

Percranial foramina and great diploetic arteries have never been reported for Lipotyphla. There is, however, an interesting con-

nection between the stapediale system and the posterior auricular in *Solenodon* (MacPhee, 1981). The fact that the connector (currently identified as a ramus posterior of the stapediale) follows a ventral, extracranial course may disqualify it from consideration as a great diploetic artery, but it would be illuminating to investigate the matter further in insectivores.

As noted earlier, loss of the mastoid foramen was regarded by Prothero et al. (1988) as a derived trait uniting all Ungulata, and these authors specifically coded this foramen as being absent in phenacodonts. Lately, Thewissen (1990) has found that the mastoid foramen is present in *Phenacodus intermedius*, although it appears to be absent in its ally *P. vortmani*. If correctly identified by Thewissen (1990), this foramen was enormous in *P. intermedius*. Russell (1964: 260) stated that the mastoid foramen is also present in *Pleurospirotherium*, albeit variable in size and position. Mastoid foramina were not encountered on the skulls of *Ectoconus* and *Meniscotherium* available to me, although once again preservation was by no means perfect. Williamson and Lucas (1992: 6) stated that a mastoid foramen is present in *Meniscotherium chamense*, but did not illustrate its location. The percranial foramen has not been reported for any condylarthrans.

14. Epitympanic sinus: (0) absent; (1) present

Morphological Discussion: See Morphology of the Cranium: Pneumatization.

Polarity Validation and Variation Within Terminal Taxa: Epitympanic sinuses are defined as variably positioned paratympanic cavities that develop from the epitympanic recess on the tympanic roof, but which do not contain any part of the ossicular chain (Van Der Klaauw, 1931). Definitional ambiguity makes it difficult to compare paratympanic sinuses across different clades, although within clades some success has been achieved in establishing character states on ontogenetic grounds (e.g., MacPhee et al., 1989; Wible, 1990). In the present case the problem is exacerbated by the great variety of epitympanic dilatations seen in members of the comparative set. Among xenarthrans they are absent only in myrmecophagids (which inflate the pterygoid/basisphenoid in-

stead) and noneuphractin dasypodids. According to Cifelli (1982: 803), in *Phenacodus* and *Meniscotherium* (and also *Proterotherium*) there is an epitympanic sinus (his "posterior petrosal epitympanic sinus") which is connected to the main tympanic cavity by a discrete pneumatic foramen. Thewissen (1985) identified a pneumatic foramen in a similar position in *Plesiorycteropus*, but as noted in the description of the cranium, the feature he described is related to the petrosal's vascularization, not its pneumatization. It is quite clear from available material that *Plesiorycteropus* lacked significant pneumatization in the temporal region, as do lipotyphlans and many other primitive eutherians (MacPhee, 1981). Hyracoids have an epitympanic sinus in their squamosals that is connected to the rest of the middle ear by a large pneumatic foramen, visible when the petrosal and bulla are dissected away from the skull. Prothero et al. (1988) apparently considered the posterior petrosal epitympanic sinus of condylarthrans to be a different feature, but here they are related as epitympanic cavitations.

15. Subarcuate fossa: (0) deep; (1) very shallow or absent (NMW 31)

Morphological Discussion: See Morphology of the Cranium: Endocranial Surface of Petrosal.

Polarity Validation and Variation Within Terminal Taxa: A deep subarcuate fossa is generally regarded as primitive for eutherians (MacIntyre, 1972; Cifelli, 1982), although the distribution of this trait is far from ideal and there can be significant variation within major clades (cf. Gannon et al., 1988). An additional problem is interobserver variation in evaluating "deep" vs. "shallow." Thewissen (1985: 264), for example, stated that the subarcuate fossa is present as a very narrow pit in *Orycteropus*, but is completely absent in *Plesiorycteropus*. In my judgement the degree of development is about the same in both, viz. negligible.

The subarcuate fossa is also small to absent in hyraxes, armadillos (slightly developed in euphractines), sloths, and manids. Myrmecophagids are polymorphic for the fossa, which is completely absent in *Myrmecophaga* but deep in *Cyclopes*. A smaller version

occurs in *Tamandua*, which collapses the argument that silky anteaters alone are anomalous among xenarthrans (cf. Novacek and Wyss, 1986a). Lipotyphlans display the primitive condition throughout. The subarcuate fossa is described as deep in *Hyopsodus* and *Arctocyon* (Gazin, 1965; Cifelli, 1982). Gazin (1965: 34) noted the presence of a "large, obtuse conical" paraflaccular fossa in *Meniscotherium* and *Phenacodus*.

16. Superior ramus of stapedia, point of exit of intratympanic portion: (0) through piriform fenestra or petrosquamosal suture; (1) through tegmen tympani; (2) none (intratympanic portion absent)

Morphological Discussion: See Morphology of the Cranium: Vascular Features.

Polarity Validation and Variation Within Terminal Taxa: All Recent ungulates either completely abort the proximal stapedia artery during prenatal life or retain no more than a thread into adulthood (Thewissen, 1985; Wible, 1987). This is true notwithstanding the fact that many and perhaps most ungulates exhibit identifiable obturator foramina in their stapes (cf. Fleischer, 1973). In lacking the proximal stapedia, extant ungulates contrast with several of their alleged relatives, including all or most condylarthrans, and a few other taxa sometimes held to be related to them, such as Tubulidentata. In tubulidentates, the ramus superior exits through a foramen in the suture or gap between the tegmen tympani and the squamosal (Thewissen, 1985), a character state which must also apply to condylarthrans that are believed to have possessed the ramus superior but display no discrete outlet for it on the tympanic roof (*Phenacodus*, *Meniscotherium*). (The apertures *tafc* and *pp ep sin* in Williamson and Lucas' [1992: fig. 6] illustration of the basicranium of *Meniscotherium* are possible candidates for a stapedia exit foramen and should be rechecked.) By contrast, in *Pleuraspidotherium* the foramen for the ramus superior is located entirely within the tegmen tympani, at least according to Thewissen's (1985) interpretation of Russell (1964). This is of interest in the present connection because in *Plesiorycteropus* the proximal stapedia (as the ramus superior) exited through an aperture in the petrosal's tegmen

tympani, not through the piriform fenestra or the epitympanic petrosquamous sinus.

Prothero et al. (1988) cited a character “[exit point of] superior ramus of stapedial in petrosal or lost” as a defining synapomorphy of a superclade Ungulata that excludes tubulidentates, but there are some problems with their analysis of this character. Prothero et al. (1988) scored the stapedial *sulcus* on the petrosal promontory as being present in mesonychids, phenacodonts, and meniscotheres—but scored the proximal stapedial *artery* as being lost in these same groups. This makes no sense, and I have considered the artery to be present in meniscotheres and phenacodonts. It should, however, be noted that conditions in *Phenacodus* are possibly ambiguous (cf. Cifelli, 1982; Thewissen, 1990).

The other derived character state in this complex is loss of the intratympanic section of the ramus superior. Loss of the intratympanic section does not imply loss of distal branches or supply areas, which are normally preserved in any case through capture of distal ramifications by other arteries (Bugge, 1974; MacPhee and Cartmill, 1986; Wible, 1987). There is good embryological evidence for the proposition that the intratympanic portion of the ramus superior has been lost in all xenarthrans and manids, at least by the adult stage (Wible, 1987). However, this says little about edentate monophyly, because this particular modification of the stapedial system is widely distributed among eutherian groups (Wible, 1987), as witness the same scoring for hyraxes.

17. Internal carotid artery, position: (0) transpromontorial; (1) perbullar; (2) extrabullar

Morphological Discussion: See Morphology of the Cranium: Vascular Features.

Polarity Validation and Variation Within Terminal Taxa: The primitive and derived character states of the internal carotid have been exhaustively examined by Wible (1986). On the basis of his analyses, *Plesiorycteropus*, *Orycteropus*, and lipotyphlans can be classed as primitive, as can myrmecophagids among xenarthrans. Dasypodids, bradypodids, megalonychids, manids (all perbullar), and hyracoids (extrabullar) are derived relative to the morphotype. For fossil taxa, carotid po-

sition has to be based on the position of an identifiable arterial sulcus. In *Meniscotherium*, the arterial course is transpromontorial (contra Williamson and Lucas [1992], who identified a “sulcus for the medial internal carotid” medial to the auditory region). It is not possible to settle the nature of carotid routing in other condylarthrans on the basis of existing information. *Phenacodus* lacks a promontorial groove even though it has a stapedial sulcus (according to Cifelli [1982], but see Thewissen [1990]). Thewissen (1985) implied that *Pleuraspidotherium* has a medially positioned internal carotid, but Russell’s (1964) description and figure clearly indicate that the artery’s position was transpromontorial. Arterial placement in *Ectoconus* appears to be unstudied.

It is appropriate to note that the Early Cretaceous therian *Vincelestes* apparently possessed a transpromontorial carotid (Rougier et al., 1992), which implies that this position is primitive at a much higher level than previously suspected.

18. Intervertebral articulations: (0) nomarthrous; (1) xenarthrous

Morphological Discussion: See Morphology of the Postcranium: Vertebral Column.

Polarity Validation and Variation Within Terminal Taxa: As is well known, Xenarthra as a group can be uniquely defined among mammals by the presence, on at least some presacral vertebrae, of true intervertebral articulations (i.e., ones involving a joint capsule) additional to those provided by the “normal” zygapophyses (Flower, 1885; Engelmann, 1978; Glass, 1985). A few mammals have dependent apophyses that vaguely mimic those of xenarthrans (*Panthera*; cf. Lessertisseur and Saban, 1967b), but as Rose and Emry (1993) pointed out, these do not participate in actual synovial joints and therefore cannot be described as “xenarthrous.” In extant *Bradypus*, only the last one or two lumbers are fully xenarthrous. However, this is clearly a case of secondary reduction rather than incipience, because extra articulations are pervasively present in the thoracolumbar series of extinct sloths (Engelmann, 1978).

The burning question concerning xenarthry is whether it is, in fact, a *shared* derived

feature of Xenarthra. Paleontologically, lack of xenarthry has been used to keep palaeo-odonts, *Ernanodon*, and a small army of other vaguely xenarthranlike eutherians out of this order (cf. review by Rose and Emry, 1993). Of special interest from the morphological standpoint is the apparent absence of any recognizable intermediate conditions between nomarthry and xenarthry (cf. Flower, 1885). Xenarthry could be viewed as a kind of "sacralization" of the lower part of the free spine, manifested by the elaboration of additional structures for contact between adjacent vertebrae. Most of what is known about sacral development is based on conditions in humans (e.g., Fawcett, 1907; Bardeen, 1910), in which chondral sacral elements form a solid mass from an early stage. This cannot be the pattern in all mammals, however, because in many taxa some or all sacral elements remain separate throughout ontogeny (Flower, 1885). I know of no case in which accessory processes have been discovered in the sacrum of any mammal, but on the other hand I know of no study in which a conscientious investigation of this point has been conducted using embryological techniques. In any case, transitory development of extra articulations in the sacrum in some non-xenarthran, should any such be found, would not necessarily "break" xenarthry as a synapomorphy of armadillos, anteaters, and sloths. But it would certainly raise this as a question, and might encourage reinvestigation of difficult problems (e.g., relationships of palaeoodonts, *Ernanodon*, *Eurotamandua*, etc.).

19. Thoracolumbar transarcual canals: (0) absent; (1) present

Morphological Discussion: See Morphology of the Postcranium: Vertebral Column, Vascular Features.

Polarity Validation and Variation Within Terminal Taxa: Because the systematic distribution of transarcual canals has not been investigated in sufficient detail in living and fossil mammals, the polarity of the character states must be considered tentative. Transarcual canals are absent in monotremes and the handful of metatherians that I have examined (table 10), and on this slender basis I infer that the presence of canals is restricted

to Eutheria. Within the comparative set, transarcual canals that strongly resemble those of *Plesiorcyteropus* in size and other features have been found only within certain Soricomorpha (see table 10, footnote b). Canals are seemingly absent in erinaceomorphs, indicating that presence of this character is by no means broadly distributed among living lipotyphlans.

In a second category there is *Orycteropus afer* and perhaps all bovids, in which tiny, nonperforating canals occur in similar locations. There is obviously room for disagreement as to whether all of these canals are homologous, and whether the state seen in orycteropodids and bovids is "incipient" or "vestigial." The fact that similar apertures occur in these last-named taxa may be evidence that this character state might be encountered more widely among ungulates sensu lato, but hyracoids, proboscideans, sirenians, perissodactyls, and the major clades of nonbovid artiodactyls apparently lack them. For the moment it can only be said that it is odd that transarcual canals have escaped detection heretofore, even in insectivores. One would think that they would have been identified long before now if they were, in fact, macroscopically obvious in any extinct or extant large group of mammals.

There is no satisfactory way of interpreting the distribution of states for this character. If possession of transarcual canals is primitive for eutherians, it is peculiar that there is almost no remaining distribution. If it is derived, it is equally odd that, as counted here, only *Plesiorcyteropus*, the aardvark, some lipotyphlans, and one family of artiodactyls exhibit this feature. At present I prefer to assume that the presence of large, perforating apertures is plesiomorphous for soricomorphs, despite the fact that they do not occur in all families. I have not been able to identify transarcual foramina in admittedly poor vertebral material of *Ectoconus*, *Phenacodus*, or *Meniscotherium*, and I conclude that they were absent. Williamson and Lucas (1992), who had access to excellent axial skeleton material of *Meniscotherium*, did not mention or illustrate transarcual vertebrae.

20. Head of humerus: (0) not extensive proximally (does not extend above tuberosities);

(1) moderately extensive proximally; (2) markedly extensive proximally

Morphological Discussion: See Morphology of the Postcranium: Humerus.

Polarity Validation and Variation Within Terminal Taxa: The head of the humerus does not usually extend above the level of the tuberosities except in highly mobile, arboreal mammals such as primates. However, there are exceptions, which means that head elevation is not exclusively tied to one kind of arboreality. Within the comparative set, manids and myrmecophagids agree with *Plesiorhycteropus* best in displaying moderate proximal extension of the head. Lipotyphlans, orycteropodids (Patterson, 1975), dasypodids, and hyraxes agree with *Hyopsodus*, *Meniscotherium* (Gazin, 1965), *Copecion* (Thewissen, 1990), *Claenodon*, *Peripitychus*, and *Ectoconus* (Matthew, 1937) in having the greater and lesser tuberosities surmount their humeral heads to varying degrees. As befits their complete commitment to the trees, the sloths have globular, almost primatelike humeral heads and are considered more derived than myrmecophagids and manids.

21. Radius and ulna: (0) distal ends subequal, broad, participate approximately equally in carpal articulation; (1) distal radius much larger, ulna strongly tapered, ulnar articular participation reduced

Morphological Discussion: See Morphology of the Postcranium: Radius; Ulna.

Polarity Validation and Variation Within Terminal Taxa: This character is very difficult to polarize. However, I am regarding subequal participation in the proximal wrist joint by the radius and ulna as primitive; the near withdrawal of the ulna from the wrist is therefore derived (cf. Lewis, 1989). In orycteropodids (Patterson, 1975), condylarthrans (Matthew, 1937), erinaceomorphs, and myrmecophagids, joint surfaces tend to be subequal and the distal ulna is not reduced. The distal radius is actually smaller in width than the distal ulna in armadillos and hyracoids, but in other respects their distal forearms are primitive in appearance. Radiocarpal joint surfaces are larger than ulnocarpal ones in soricomorphs (unless greatly modified for digging; Reed, 1951), sloths, and manids, and therefore they are derived in the same direc-

tion as *Plesiorhycteropus*. This spread of taxa suggests that this character is not substantially tied to a single functional category.

22. Pubic symphysis: (0) unreduced; (1) highly reduced

Morphological Discussion: See Morphology of the Postcranium: Innominate.

Polarity Validation and Variation Within Terminal Taxa: The highly to completely reduced pubic symphysis, found in most soricomorph and erinaceomorph insectivores, is considered by MacPhee and Novacek (1993) to be a probable synapomorphy of Lipotyphla. Reduction, not involving complete loss, occasionally occurs outside Lipotyphla, but almost exclusively among mammals that are diggers. The majority of xenarthran taxa and pholidotans are within this functional grouping. It is of interest that living sloths—certainly not fossorial mammals—also possess small symphyses, which implies that symphyseal reduction is a xenarthran character. Hyraxes exhibit very long symphyses and are thus primitive. In all condylarthrans for which there is significant evidence of pelvic construction, the pubic symphysis is actually quite elongate (cf. Gazin, 1965). For example, in *Meniscotherium terraerubrae* AMNHP 48002, the total length of the innominate (iliac crest to ischial tuberosity) is 126 mm, while the length of the pubic symphysis is 42 mm (33% of total innominate length). By contrast, the symphysis is only a small fraction of “total” innominate length in bibymalagasy (3%, using values for ILH and ISL in table 12). In *Orycteropus*, the equivalent figure is 17%, which might be interpreted as borderline but is here considered primitive.

23. Sacral-innominate fusion: (0) absent; (1) present, with complete or nearly complete closure of ischiatic notch to form sacroischiatic foramen (NMW 69)

Morphological Discussion: See Morphology of the Postcranium: Innominate.

Polarity Validation and Variation Within Terminal Taxa: Novacek et al. (1988) argued that xenarthrans and pholidotans closely correspond in several pelvic features related to the intimate connection of the sacrum and ischium. In xenarthrans other than *Cyclopes*, the transverse processes of the last several

pseudosacrals fuse to the medial aspect of the ischia, thus circumscribing a bony "sacroischiadic [sic] foramen." In pholidotans they do not fuse, but are in strong ligamentous connection. *Tamandua* and *Myrmecophaga*, in which fusion is often less complete, and *Cyclopes*, in which it does not occur at all, show the strongest shape similarity to *Manis*.

The parallel between (some) xenarthrans and pholidotans in pelvic organization is interesting but should not be overinterpreted. In some respects pelvic organization in manids does not depart greatly from the standard eutherian pattern. For example, sacrotuberous and sacrospinous ligaments are present and help to define separate (arthrological) greater and lesser sciatic foramina. In armadillos and sloths, there is no free ischiatic border, the ligaments are absent (or replaced by bone), and therefore the arthrological lesser sciatic foramen is lacking. (The greater sciatic foramen is present, as the sacroischiatic foramen, completely ringed by bone.) One result of this configuration is that muscles and other structures that are conducted through the lesser sciatic foramen in typical eutherians are repositioned in armadillos, anteaters, and sloths. For example, in these edentates there is no intrapelvic portion of the obturator internus, the apparent homolog of this muscle arising in a unit mass with the gemelli (Windle and Parsons, 1899; Jouffroy, 1971a). Manids presumably have a typical intrapelvic origin for this muscle, despite the assertion of Windle and Parsons (1899) that all *Edentata lack this portion. Although extant manids show a high degree of iliosacral fusion, *Patriomanis* (USNM 299960) does not, which could suggest that the condition found in living pangolins is not primitive for the family. Ischiosacral fusion or ossification of connecting ligaments sporadically occurs in other eutherians (*Scapanus*, *Geomys*, *Tragulus*, *Pteropus*; Rose and Emry, 1993). All this suggests that there is no strong reason to code pangolins as being derived for this character, contra Novacek et al. (1988).

This is a difficult trait to rate in *Plesiorcyteropus*, in part because the evidence for pelvic organization in this taxon is poor. Despite the very close approximation of pseudosacrals and ischial rami, there is no evidence for sacroischiatic fusion. It might be argued

that the "highly approximated" condition, as seen in *Cyclopes*, is primitive for Xenarthra but derived among eutherians overall. This might permit the logical extension that sacroischiatic approximation is a shared derived feature of Xenarthra + *Plesiorcyteropus* (or some larger grouping including manids). However, Engelmann (1978) argued strongly for the view that sacroischiatic approximation in *Cyclopes* is secondarily derived rather than primitive. I follow him in this and therefore score *Plesiorcyteropus* as plesiomorphic.

24. Lateral process of ischium: (0) absent; (1) present

25. Ischial expansion: (0) absent; (1) present

Morphological Discussion: See Morphology of the Postcranium: Innominate. See also Function, Adaptation, and Extinction: Pelvic Adaptations.

Polarity Validation and Variation Within Terminal Taxa: The lateral process of the ischium is arguably linked to character 25, but it is included here because it is one of the very few highly derived—but narrowly distributed—features of *Plesiorcyteropus* and *Orcyteropus* actually identified by Patterson (1975).

As discussed in the descriptive sections, the lateral process is definitely rare among extant mammals and is apparently absent in all members of the comparative set other than *Orcyteropus*. In anteaters, sloths, hyraxes, and most other eutherians, the origin for biceps and semitendinosus is usually marked by no more than a shallow depression, not a prong-like outgrowth. In pangolins the caudal rim of the ischium is everted, but there is no distinct lateral process. This is also the case in soricoids and golden moles (*Chlorotalpa*, *Amblysomus*). The "posteroventral [postero-dorsal] process of the ischium," described by Frost et al. (1991) for some erinaceids, is in reality a caudal elongation of the ischial tuberosity and is therefore not a separate lateral process. Gazin (1965: 65) described the ischial tuberosity of *Meniscotherium*, *Phenacodus*, and *Hyopsodus* as "prominently developed," but, as illustrations and actual specimens make clear, this simply means that it was rostrocaudally elongate.

In the morphological description I noted

that the process is not situated in precisely the same position in armadillos and bibymalagasy, and, moreover, in *Orycteropus* it is not associated with ischial expansions. No known condylarthran has expanded tuberosities in the sense used here, nor do any derived ungulates with the exception of chalicotheres (in which expansion appears to be an autapomorphy of one genus). Morphologically, the expansions resemble the support buttresses for the carapace in armadillo. However, there is no evidence of a positive sort for the presence of bony armoring in bibymalagasy; keratinous dermal armoring on the model of pangolins cannot be ruled out, but there is nothing that makes it particularly likely. The functional interpretation proffered in the section on adaptations—that the ischial expansions were covered in life by sitting pads—is also tentative.

I admit to severe reservations about this character. The modern posture is to assert that homology and convergence cannot be sorted out aprioristically, but only in the context of a given phylogenetic statement. In cases where one can draw on large numbers of characters, inclusion of a few that are of doubtful homology is perhaps permissible. When the data set is as small as the one under review here, it is a more serious problem. On the other hand, there are correspondences between conditions in bibymalagasy and armadillos that cannot be ignored merely because an inference of homology would raise difficult phylogenetic and biogeographical questions. It seems to me that the shape similarities and operational homology have to prevail in this case, unless it can be shown through a highly resolved phylogeny that homoplasy is the better conclusion.

26. Lesser trochanter of femur: (0) small or not markedly excavated on caudal surface; (1) large and deeply excavated on caudal surface (for quadratus femoris)

Morphological Discussion: See Morphology of the Postcranium: Femur.

Polarity Validation and Variation Within Terminal Taxa: The lesser trochanter tends to be small and conical in most eutherians and metatherians; it assumes a flattened, flared form in comparatively few eutherian taxa (cf. Lessertisseur and Saban, 1967b;

Beard, 1993). With the exception of dasypodids, xenarthrans have rather small lesser trochanters, as do all orycteropodids, manids, most lipotyphlans (exception: *Desmana*), *Hyopsodus* (Gazin, 1968), and some other condylarthrans (e.g., *Tetraclaenodon*; Radinsky, 1966). In dasypodids, the lesser trochanter is usually large but not excavated by muscular origins. By contrast, *Plesiorhycteropus*, *Meniscotherium*, *Ectoconus*, and hyracoids (Le Gros Clark and Sonntag, 1926; Matthew, 1937; Gazin, 1965) all display a similar configuration of lesser trochanter size and rugosity that carries over even into small details of construction, such as the semicircular crest that defines the distal limit of the fossa for the quadratus femoris. Trochanteric similarity is strong enough in these cases to raise the possibility of homology.

27. Fovea for ligamentum teres: (0) does not interrupt margin of articular surface of femoral head; (1) interrupts margin; (2) absent

Morphological Discussion: See Morphology of the Postcranium: Femur.

Polarity Validation and Variation Within Terminal Taxa: The fovea tends to be subcentral in most mammalian groups (when present), and this is therefore considered to be the primitive state. In a very few extant groups the fovea is set so far posteriorly that it interrupts the margin of the head; Lessertisseur and Saban (1967a) recorded this feature for tubulidentates, hyracoids, perissodactyls, and *Dasypros* (to which may now be added *Euphractus*, *Priodontes*, *ChaetophRACTUS*, and *Tolypeutes*, indicating that it is the general condition in dasypodids). The degree of interruption is not precisely the same in all of these cases. In dasypodids and hyracoids, the fovea is quite shallow but nevertheless broadly interrupts the posterior margin of the head. In armadillos the pit is much deeper and just intersects the capital margin. This is also true of *Plesiorhycteropus*, and appears to apply as well to *Meniscotherium* and *Phenacodus* (Gazin, 1965; Williamson and Lucas, 1992). Thewissen and Domning (1992) do not concur in the scoring of their similar character 45, but the interruption of the margin is clearly marked in *Meniscotherium chamense* (cf. fig. 24B of Williamson and Lucas, 1992). All of these cases contrast markedly

with lipotyphlans and myrmecophagids (fovea often deep and subcentral) and living manids and sloths (fovea absent). The femoral head of *Patriomanis* USNMP 299960 is definitely foveate, but the pit does not seem to extend to the margin (cast damaged in this area).

28. Astragalus, separate cotylar fossa for medial malleolus: (0) absent; (1) present

Morphological Discussion: See Morphology of the Postcranium: Tibia and Fibula; Astragalus.

Polarity Validation and Variation Within Terminal Taxa: *Orycteropus* differs from *Plesiorhycteropus* in that the condylar facet of the medial malleolus is substantially less convex and less projecting, and faces more laterally than medially. As a result, the cotylar facet of the astragalus is shallower, impinges less on the astragalar neck, and is practically coplanar with the medial keel of the trochlea (vs. being set at a near right angle in bibymalagasy). Conditions in *Leptorycteropus* are not known, but in *Myorycteropus* the cotylar fossa appears to be completely absent (cf. MacInnes, 1956).

Gregory (1910: 363) mentioned that the "step-like articulation" (i.e., cotylar fossa) of the hyracoid astragalus may have been derived from a condition like that exhibited "in *Meniscotherium* in which the tibia articulated chiefly with the internal side of the astragalus." I find that the cotylar fossa is present in *Meniscotherium*, although it is not nearly so strongly indicated as it is in *Plesiorhycteropus* and hyraxes. Unfortunately, the relevant area is not described by Williamson and Lucas (1992). The fossa is absent in all of the other condylarthrans considered here, but not necessarily in other primitive ungulates.

The cotylar fossa has a limited distribution among eutherians and on this basis is considered derived within that group (cf. Lewis, 1989). Its correlation with locomotor habitus remains elusive. A cotylar fossa is present in many Old World monkeys (e.g., *Macaca*, *Colobus*), suggesting a possible connection with arboreal adaptation (cf. Lewis, 1989).

29. Astragalus, posteromedial process: (0) very small or absent; (1) large

Morphological Discussion: See Morphology of the Postcranium: Astragalus.

Polarity Validation and Variation Within Terminal Taxa: Many eutherian astragali display a small protuberance on the proximointernal margin of the astragalus. It is therefore important to distinguish the primitive case, in which any such projection is negligible, from the derived condition, in which it is quite prominent. In this analysis I shall tentatively treat all prominent occurrences of the posteromedial process as homologous, but it should be noted that there are at least two distinct evocations of this character state among eutherians. In the one, the posteromedial process bears an extension of the trochlear articular surface, indicating that in this case the process functions as an additional support pillar for the tibia. In the other derived state, the support function is not evident because the tibial facet does not spread over onto the process. In *Plesiorhycteropus* it is clear that the posteromedial process acted as a muscle pulley, but in most of the other cases referenced below, positive evidence for this—an identifiable tendon groove—is lacking.

In manids and xenarthrans, the medial margin of the astragalus lacks distal protuberances; it either forms an essentially flat wall or is actually undercut in the relevant area. Each of these taxa is considered primitive for this character. This is also true of erinaceomorphs, although in the talpid soricomorph *Desmana* there is a definite distal protuberance (directed plantarward rather than medialward, and probably for flexor fibularis only). In *Orycteropus afer* and *O. gaudryi*, there is a very prominent posteromedial process, onto which the trochlear facet extends. In *Myorycteropus*, however, this process is negligible (cf. MacInnes, 1956). In hyraxes, the entire medial aspect of the trochlea is converted into the cotylar fossa, and the posteromedial process as a distinct entity is not present.

In *Meniscotherium* and *Ectoconus* there is a small posteromedial process, but even in well-preserved specimens (e.g., AMNHP 4414, 17075) there is no indication of a ven-

tral groove. This process is lacking on the astragalus of *Hyopsodus* (Gazin, 1968) and also on that of *Phenacodus* (e.g., AMNHP 15262), despite the latter's overall strong resemblance to the astragalus of *Orycteropus*.

30. Ungual phalanges: (0) nonspatulate; (1) spatulate

Morphological Discussion: See Morphology of the Postcranium: Phalanges.

Polarity Validation and Variation Within Terminal Taxa: Nonspatulate ungual phalanges are considered primitive on the basis of their presence in most marsupials and many eutherian orders, including lipotyphlans. Spatulate but not necessarily hooflike unguals are found in tubulidentates, hyracoids, and most condylarthrans, with the usual prominent exception of *Hyopsodus* (see Williamson and Lucas, 1992). Fissuring, not found in *Plesiorhycteropus*, occurs in several groups, including manids (phalanges compressed) and *Ectoconus* (phalanges broadened).

31. Mandible: (0) unreduced; (1) highly reduced and edentulous

32. Zygomatic arch: (0) uninterrupted; (1) interrupted

Morphological Discussion: See Morphology of the Cranium: Infratemporal Fossa; Craniomandibular Joint.

Polarity Validation and Variation Within Terminal Taxa: Because the hypodigm of *Plesiorhycteropus* is seriously incomplete in some ways, it is of some interest to consider how character states imputed to bibymalagasy by Patterson (1975) affect assessment of its phylogenetic relationships. His basis for inferring the presence of derived states of these characters in bibymalagasy is not supported by direct evidence and is fully discussed elsewhere (See Introduction and Morphology of the Cranium).

REJECTED CHARACTERS

The number of characters not considered in this monograph is, of course, infinite. The following notes refer mainly to characters that have achieved a certain currency in recent years because they appear in highly referenced papers.

A. Mandibular fossa limited to processus zygomaticus of squamosal

This character summarizes Patterson's (1975) morphological observations on the mandibular fossa of *Plesiorhycteropus*, considered here to be incorrect. Under Patterson's interpretation, *Plesiorhycteropus* and pholidotans display what would currently be regarded as a highly derived state not found in any other member of the comparative set or elsewhere in Mammalia. In fact *Plesiorhycteropus* autapomorphously displays another derived state, mandibular fossa completely limited to facies articularis of squamosal.

B. Foramen ovale completely enclosed within alisphenoid, not notched into posterior margin of this element (NMW 34)

According to Novacek and Wyss (1986a), myrmecophagids, bradypodids, and pholidotans lack this derived trait and display instead a more primitive condition, in which the foramen simply notches the posterior border of the alisphenoid. Rose and Emry (1993) argued that this is incorrect, and that in all three groups the prevalent pattern is to form the walls of the foramen from alisphenoid material. Other local bones (chiefly the squamosal and pterygoid) may overlap the alisphenoid, but their participation in foraminal walls is superficial. Rose and Emry's (1993) observations accord with mine, although I found it difficult to ascertain conditions in many adult xenarthrans because of sutural obliteration. In any case, we seem to be dealing here with a distinction without a difference.

C. Glaserian fissure distinct, elongate trough on anterolateral wall of the tympanic cavity (NMW 87)

In my experience, glaserian fissures are only "distinct" when there is an inflated bulla that narrows the gap through which the chorda tympani escapes, but some other morphological concept must be intended here because the distribution of this character is said by Novacek and co-workers to be limited to insectivores and armadillos (both primitively abullate) and hyracoids (which possess bullae).

D. Large mastoid tubercle (incorporates tympanohyal) nearly reaches lateral edge of promontorium cochleae (NMW 88)

Tympanohyals almost always “nearly” reach the promontorium when they can be observed, and I regard this as a eutherian (or therian) symplesiomorphy. Further, it is often difficult to tell in adult skulls whether the “mastoid process” derives from the petrosal, tympanohyal, or squamosal, or any combination thereof.

E. Ventral, slitlike aquaeductus cochleae (PMF 3)

Whether or not the cochlear canaliculus (aquaeductus cochleae) is ventrally visible seems to have less to do with the actual position of the canaliculus than with the size of the posterior lacerate foramen through which it is viewed. In *Plesiorhycteropus* the aperture of the cochlear canaliculus is externally visible on the lateral wall of the large posterior lacerate foramen and would therefore presumably be considered “ventral” in position. However, it lies at the base of a deep concavity, and cannot be described as a slit. According to Cifelli (1982), *Procavia* is somewhat similar in that the aperture of the canaliculus is ventrally positioned but not slitlike, which I confirm. (Unlike Prothero et al., [1988], Cifelli defined “ventral aquaeductus cochleae” and “slit aquaeductus cochleae” as separate characters.) On the whole I regard this character to be of very uncertain polarity and difficult to divide into useful or consistently interpretable character states.

F. Tympanic aperture [of] facial canal anterior to fenestra ovalis (PMF 5)

This character is coded by Prothero et al. (1988) as present in all ungulate taxa for which it was possible to take an observation, with the prominent exception of artiodactyls. I regard the character as a poor one, since I contend that the *position* of foramen faciale varies not because the facial nerve follows different pathways through the middle ear, but because the postforaminal conduit it travels within is variably ossified. In any case, an anterior (or anterodorsal) position of foramen faciale (i.e., a completely unossified facial canal) is surely primitive rather than derived, and I dispute the polarity of this character.

G. Large, bridged tympanohyal (PMF 6)

The “bridge” in this instance does not refer to the frequently observed contact between the tympanohyal and the caudal tympanic process of the petrosal, but instead to tympanohyal-*squamosal* contact. This feature is well defined, but was not used here because it is restricted among ungulates to perissodactyls and hyraxes (and therefore would merely show up as a hyracoid autapomorphy).

H. Lose stapedial sulcus (PMF 8)

See Character 16.

I. Inflated tegmen tympani (PMF 4)

This character is logically subsumed by my character 11, unless one has a method for distinguishing an inflated tegmen from one that is merely large. However, I will note that the *internally* pneumatized tegmen tympani of some ungulates, as described by Cifelli (1982), is definitely absent in *Plesiorhycteropus*. It is also absent in *Orycteropus*, although the shape of the tegmen in the latter is quite definitely affected by pneumatization of the epitympanic recess.

J. Tibia and fibula fused proximally and distally

Although thoroughgoing fusion of the proximal and distal ends of the leg bones is rare, the one functional grouping that displays double fusion with some frequency is diggers (Barnett and Napier, 1953). As noted, dasypodids and bibymalagasy correspond rather markedly in other details of the bones concerned, but the palaeonodonts *Xenocranium* and especially *Dipassalus* are not phenetically far removed (cf. Rose et al., 1991). With regret, I consider this character and many others of a similar sort (e.g., projecting deltoid eminence, enlarged medial epicondyle, elongate olecranon process, elongate greater trochanter) to be of low valency in the context of this investigation.

ANALYTICAL RESULTS USING THE 30- AND 32-CHARACTER MATRICES

The next three sections concern the interpretation of the results of specific PAUP 3.0s runs utilizing the 30CM or 32CM. Output, in the form of cladograms (most parsimonious [MPTs], strict consensus, and 50% ma-

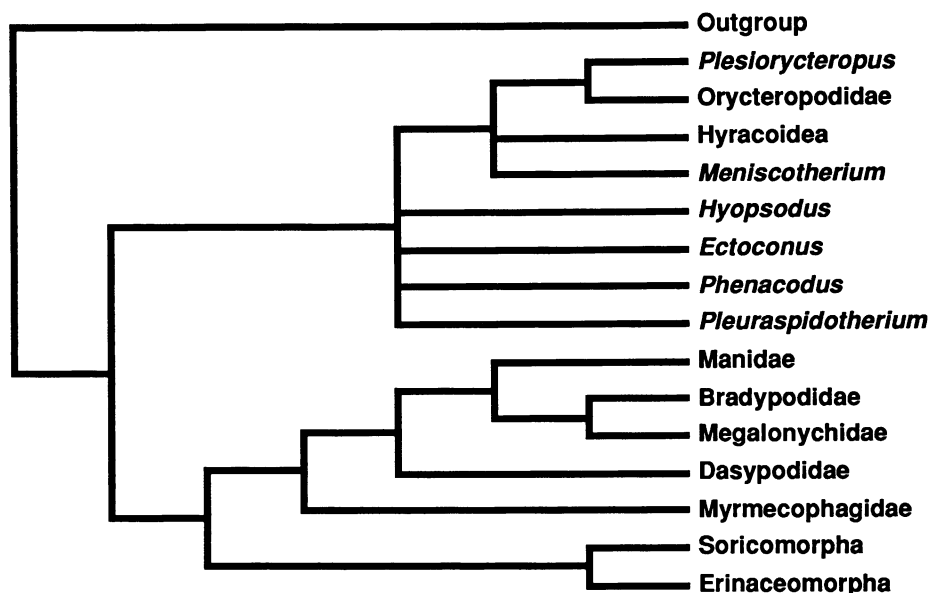


Fig. 48. Strict consensus diagram for 21 MPTs derived from parsimony analysis of 30CM (table 18), all taxa included (TL = 74, CI = 0.46, RI = 0.64; branch-and-bound routine). All MPTs include the clades *Plesiorycteropus* + Orycteropodidae, Lipotyphla (Soricomorpha and Erinaceomorpha) and *Edentata (but note Manidae is nested against sloths); they differ only in the position of individual condylarthran taxa and hyracoids. The sister group of *Plesiorycteropus* + Orycteropodidae is either Hyracoidea or *Meniscotherium* (see fig. 49).

jority rule), is reproduced in figures 48–55, together with tree lengths (TLs), retention indices (RIs), and consistency indices (CIs, using informative characters only). Partial lists of apomorphies by stems (nodes) for various runs are supplied in tables 19–22; a complete list is provided in table 23 for the phylogeny depicted in figure 51A. Solutions under acctran (accelerated character optimization, with reversals preferred over parallelisms) and deltran (delayed character optimization), if different, are also noted. Phylogenetic parsimony programs are now widely available, and readers can access additional information or examine different manipulations simply by running the data matrix themselves.

In group A analyses, no phylogenetic assumptions are employed additional to the ones that were used to create the taxon list and undertake the character analysis in the first instance. In group B analyses, constraints are added in order to examine how different imposed phylogenies affect results. In group C analyses, the taxon list is restricted to the forms investigated by Lamberton (1946) and Patterson (1975), in order to illustrate the

effect of such restrictions on results when the data are as messy as they are in the present case.

GROUP A RUNS: NO ASSUMPTIONS

In the runs reported in this section, no assumptions are made about relationships and there are therefore no constraints on topology. Examination of the 30CM (table 18) reveals no obvious pattern to the distribution of potential synapomorphies: seven derived character states found in *Plesiorycteropus* co-occur in hyracoids, six in Dasypodidae and Orycteropodidae, and four in Manidae.

Operating on the 30CM and complete taxon list, PAUP yields 21 MPTs using the branch-and-bound routine with the “furthest” addition option in effect (see figs. 48 and 49 for additional information). As may be inferred from the strict consensus diagram (fig. 48), there is a certain amount of invariant structure in these trees, with *Plesiorycteropus* + Orycteropodidae, Lipotyphla, and a clade incorporating Xenarthra and Manidae appearing in 100% of trees. In all trees, the dyad

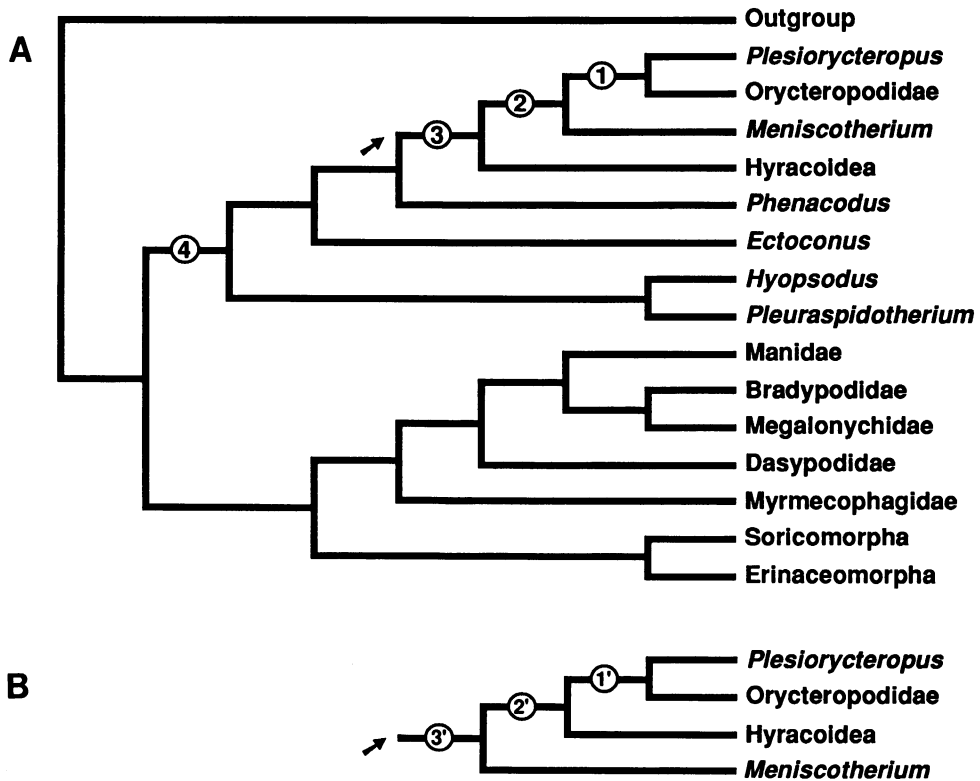


Fig. 49. Two of 21 MPTs referenced in figure 48, differing only in the taxon occupying the role of sister group of *Plesiorycteropus* + *Orycteropodidae*. Numbered stems are described in tables 19 and 20. In tree 1 of the original run (A), the sister taxon of *Plesiorycteropus* + *Orycteropodidae* is *Meniscotherium*. In tree 4 of original run (B), the sister taxon is *Hyracoidea*; proximal to the arrows, branches are the same in the two trees. In all trees, stem 1 (*Plesiorycteropus* + *Orycteropodidae*) collects the same three transformations: C 13, reappearance of percranial foramen canal (reversal); C 19, transarcual canals; and C 24, lateral process of ischium. By contrast, only a single transformation is unambiguously placed on stem 2 (supporting sister taxon of *Plesiorycteropus* + *Orycteropodidae*). In A, *Meniscotherium* is supported as the sister taxon by C 29 (stem 2, posteromedial process of astragalus); in the alternative arrangement in B, *Hyracoidea* is supported by C 15 (stem 2'; shallow/absent subarcuate fossa). Two unambiguously placed transformations are on the unnumbered stem joining *Edentata and Lipotyphla (C 9, pterygoid tympanic process, and C 22, pubic symphysis reduction), but there is only a single transformation on stem 4 (C 5, lacrimal foramen).

Plesiorycteropus + *Orycteropodidae* is supported by three transformations (C 13, reappearance of percranial foramen canal [reversal]; C 19, transarcual canals; C 24, lateral process of ischium, the last of which is unique). Further inspection of individual MPTs reveals that between-tree differences in taxon positionings are entirely due to rearrangements of *Hyracoidea* and taxa traditionally grouped as condylarthrans. Setting aside the condylarthran rearrangements and concentrating on *Plesiorycteropus* and its

closest relatives, we find that there are really only two basic deployments of taxa (fig. 49A, B): the sister group of *Plesiorycteropus* + *Orycteropodidae* is either *Hyracoidea* or *Meniscotherium*. But the support for either arrangement is very thin, for only a single character is unambiguously placed at the node in question (table 19, stem 2; table 20, stem 2').

Taxa within *Edentata form unlikely groupings in most runs reported in this chapter (e.g., *Manidae* consistently appearing be-

TABLE 19
Apomorphy List for Selected Stems, Figure 49A^{a,b}

Location	Apo- mor- phies ^c	Transformations
Stems (nodes)		
4	1	5; (D13); (A13)
3	3	7, 11, 28
2	1	15
1	3	13, 19, 24
Terminal taxa		
<i>Plesiorhycteropus</i>	10	1, 6, 9, 14, 16, 20, 21, 22, 25, 30; (D29)
Orycteropodidae	5	5, 7, 10, 11, 26
Hyracoidea	4	4, 12, 16, 17 ; ((A29))
<i>Meniscotherium</i>	1	10; (D29)

^a See figure 49 for location of numbered stems.

^b Key: Roman: unequivocally placed transformations from primitive to derived (0 → 1 or 2) or derived to derived (1 → 2 or 2 → 1); italics: unequivocally placed transformations from derived to primitive (reversion, 1 or 2 → 0). Boldface: transformations having character CIs of 1.00. In parentheses: ambiguously placed transformation from primitive to derived; in double parentheses: reversion. Letters A (acctrans) and D (deltrans) indicate which optimization regime locates the character on a given stem.

^c Number of apomorphies that are unequivocally placed on stems indicated.

tween sloths and other xenarthrous taxa). However, as the focus is not on xenarthran relationships in this study, I will continue to use *Edentata without implying a specific scheme of relationships for taxa contained therein.

In Characters and Transformations I expressed my concern about the accuracy of character-state scoring for certain taxa. To see what effect alternative scoring might have in a specific case, I changed character states from 0 to 1 under *Pleuraspidotherrum*, *Phenacodus*, and *Meniscotherium* for C 12 (mastoid exposure). The 30CM, thus revised, was run with the complete taxon list. The strict consensus of 25 MPTs (heuristic search; TL = 75, CI = 0.45, RI = 0.63) yielded only *Edentata and Lipotyphla as constant groupings, although *Plesiorhycteropus* + Orycteropodidae appeared in 80% of trees.

As has been demonstrated in a number of different contexts (for a short review, see No-

TABLE 20
Apomorphy List for Selected Stems, Figure 49B^{a,b}

Location	Apo- mor- phies ^c	Transformations
Stems (nodes)		
4	1	5; (D13); (A13)
3	3	7, 11, 28 ; (A15)
2	1	29; (A10)
1	3	13, 19, 24 ; (D15)
Terminal taxa		
<i>Plesiorhycteropus</i>	10	1, 6, 9, 14, 16, 20, 21, 22, 25, 30; ((A10))
Orycteropodidae	4	5, 7, 11, 26; (D10)
Hyracoidea	4	4, 12, 16, 17 ; (D15)
<i>Meniscotherium</i>	0	((A15)); (D10)

^a See figure 49 for stem location.

^b Key: see table 19.

^c See table 19, footnote c.

vacek, 1992a), fossil taxa—especially incompletely known fossil taxa—can have a decided effect on branching patterns. That is certainly the case here, as is easily demonstrated by removing condylarthrans. Run without the condylarthran data, the 30CM

TABLE 21
Apomorphy List for Selected Stems, Figure 50B1^{a,b}

Location	Apo- mor- phies ^c	Transformations
Stems (nodes)		
2	1	27; (D15); (A14, 19, 24, 28 , 30)
1	4	5, 7, 11, 26 ; (D28); (A16)
Terminal taxa		
<i>Plesiorhycteropus</i>	8	1, 6, 9, 20, 21, 22, 25, 29; (D16, 19, 24); ((A14, 30))
Orycteropodidae	1	10 ; (D14, 19, 24, 30)
Hyracoidea	5	4, 12, 13, 16 ^d , 17 ; (D14, 16, 30); ((A19, 24))

^a See Figure 50B1 for stem location.

^b Key: see table 19.

^c See table 19, footnote c.

^d Derived-derived transformation.

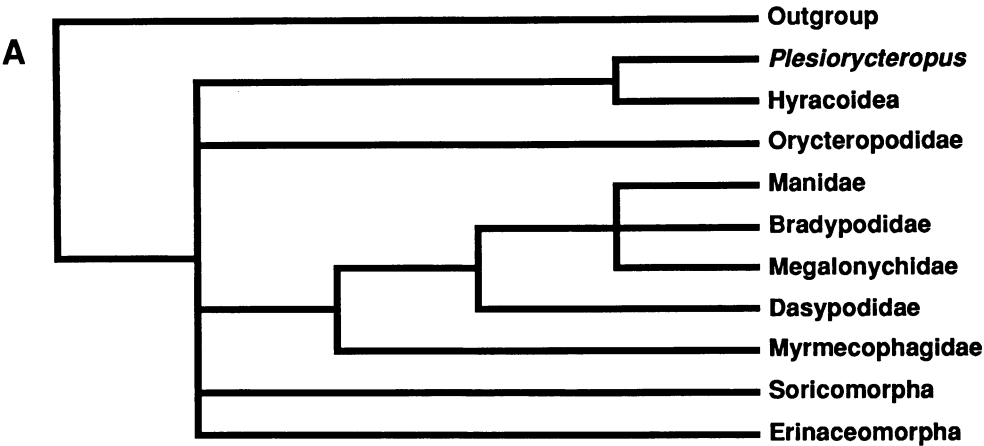


Fig. 50. Strict consensus diagram (A) for 8 MPTs (B1-B8) derived from parsimony analysis of 30CM (table 18), all condylarthran taxa excluded (TL = 66, CI = 0.52, RI = 0.56; branch-and-bound routine). Numbered stems in B1 and B7 are described in tables 21 and 22. In all eight MPTs, Hyracoidea is the sister taxon of *Plesiorycteropus*; this dyad is supported by four unambiguously placed characters in both B1 (C 5, 7, 11, 26) and B7 (C 5, 11, 26, 28). Position of Orycteropodidae is variable, but it is sister to *Plesiorycteropus* + Hyracoidea in only one tree (B1, stem 2 supported by a single unambiguously placed transformation, C 27).

data matrix yields 8 MPTs of 66 steps (fig. 50A, B). *Edentata is preserved in all MPTs, while Lipotyphla is retained in 7 of the 8 MPTs. However, the dyad consisting of *Plesiorycteropus* + Orycteropodidae—found in all 21 MPTs in the first run (fig. 48)—is not represented at all, the sister position having been

taken by Hyracoidea in 100% of the MPTs. This presumably happened because certain derived features that previously helped to pull Hyracoidea into the condylarthran pool no longer do so, while others now act to pull hyracoids toward *Plesiorycteropus*. In figure 50B1, the stem supporting *Plesiorycteropus* + Hyracoidea is defined by four unequivocally placed synapomorphies (C 5, 7, 11, 26), two of which are uniquely transformed (table 21). In figure 50B2, the equivalent stem is also defined by four unequivocally placed synapomorphies (C 5, 11, 26, 28), three of which are unique transformations in this particular evocation of most-parsimonious relationships.

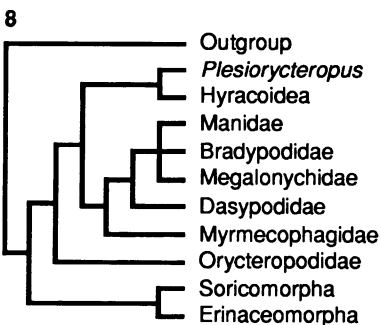
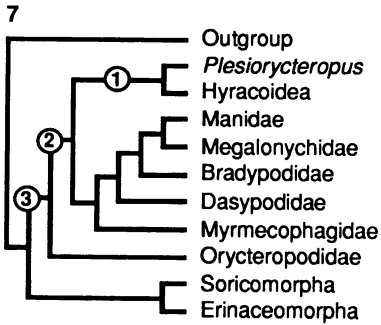
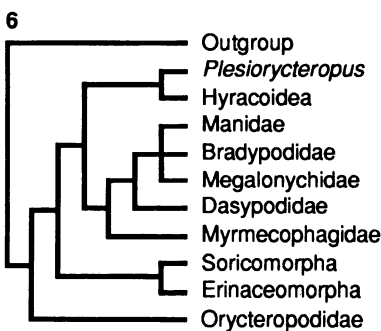
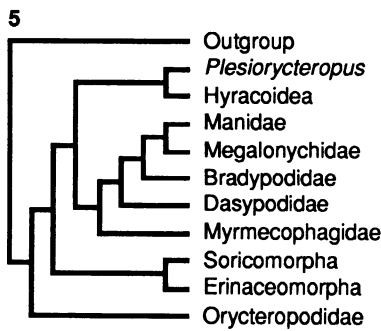
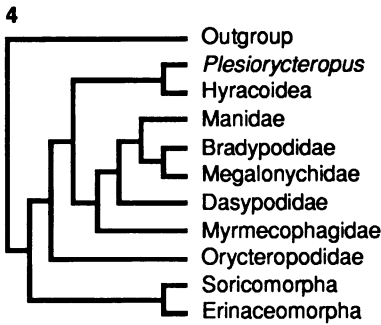
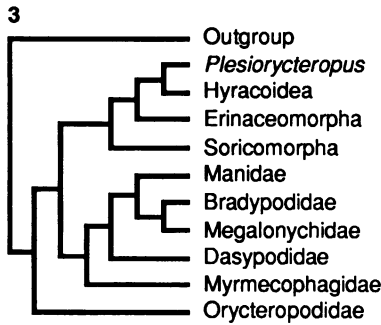
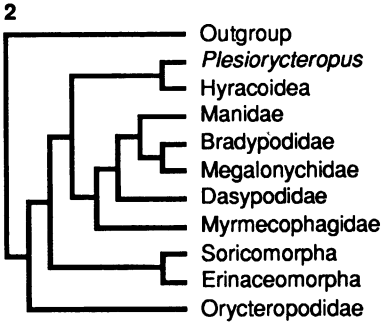
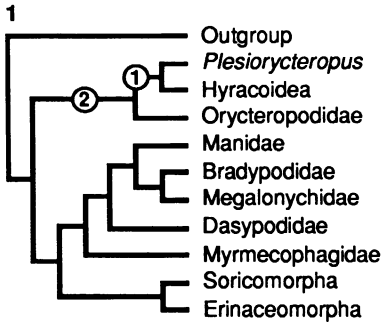
How different is this solution from ones that are only slightly less parsimonious? With the same taxon list, PAUP collects 38 trees at 67 steps. Topologies vary, but in not one instance is Orycteropodidae the exclusive sister group of *Plesiorycteropus*. (By contrast, Hyracoidea is included in the sister taxon of *Plesiorycteropus* in 89% of trees (34/38), either alone [31 trees] or in combination with Orycteropodidae [3 trees].) *Plesiorycteropus* + Orycteropodidae appears as an exclusive grouping only at TL = 68, and then in only 2% of all trees (4/174). It seems that, with this data matrix, sister-group relationships

TABLE 22
Apomorphy List for Selected Stems, Figure 50B7^{a,b}

Location	Apo- mor- phies ^c	Transformations
Stems (nodes)		
3	2	15, 27; (A14)
2	2	7, 16; (A12)
1	4	5, 11, 26, 28
Terminal taxa		
<i>Plesiorycteropus</i>	9	1, 6, 16, 19, 20, 21, 24, 25, 29; (D9, 22); ((A12, 14))
Orycteropodidae	4	10, 19, 24, 30; (D14); ((A9, 22))
Hyracoidea	4	4, 13, 17, 30; (D12, 14); ((A9, 22))

^a See Figure 50B7 for stem location.
^b Key: see table 19.
^c See table 19, footnote c.

B



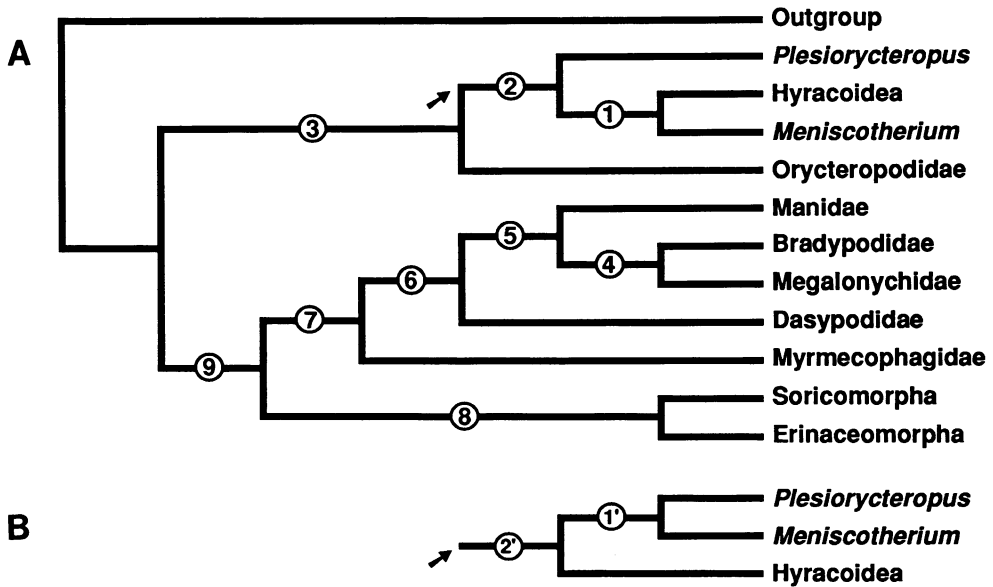


Fig. 51. Two MPTs (A, B) are recovered from parsimony analysis of 30CM (table 18) when all condylarthran taxa except *Meniscotherium* are excluded (TL = 69; CI = 0.49; RI = 0.59; branch-and-bound routine). Transformations collected at numbered stems are fully described in table 23. The MPTs differ only in regard to the sister taxon of *Plesiorcyteropus* (Hyracoidea + *Meniscotherium* or *Meniscotherium* alone), so only branches distal to stem 2' (arrow) are reproduced in B.

for bibymalagasy are strongly influenced by choices to include or omit fossil evidence.

GROUP B RUNS: MEASURING THE EFFECT OF CONSTRAINTS

In Group A runs, taxa were permitted to combine unrestrictedly, forming associations solely on the basis of the information in the data matrix. A different approach is to assume that some relationships within the taxon set are known a priori. The PAUP topological constraint option permits the imposition of a partial phylogenetic resolution during the parsimony calculation, thereby permitting one to observe how remaining (unconstrained) taxa perform. This routine is an efficient way of judging the relative “cost” of adopting cladistic solutions that might differ from one(s) found with no constraints in place.

Because it is clear from Group A runs that taxon deletions have a profound effect on outcomes, a decision has to be made about the inclusiveness of the taxon set. On the one hand, it seems unjustifiable to permit output results to be seriously affected by taxa with

limited information content (i.e., fossils). On the other hand, in view of the similarities that some of the better-known condylarthrans display to *Plesiorcyteropus*, it seems equally unjustified to remove them entirely from consideration. Unfortunately, since the monophyly of *Condylarthra is itself an unresolved systematic issue, utilization of a condylarthran morphotype or “hypothetical taxonomic unit” would be logically fraudulent. There can be no happy solution here, and my compromise is to retain *Meniscotherium* (a condylarthran taxon for which information is relatively complete) and to delete the rest.

With the taxon list depleted as described and with no constraints in place, parsimony analysis of the 30CM yielded two MPTs (fig. 51A and B, table 23; one tree, identical to fig. 51A, was recovered if *Meniscotherium* was scored as 1 rather than 0 for C 12). Results were compared to results of four other runs, in which constraints were enforced (table 24). The edentate and xenarthran constraints embody well-known systematic hypotheses and are self-explanatory. The aardvark/insectivore constraint embodies the proposal (see

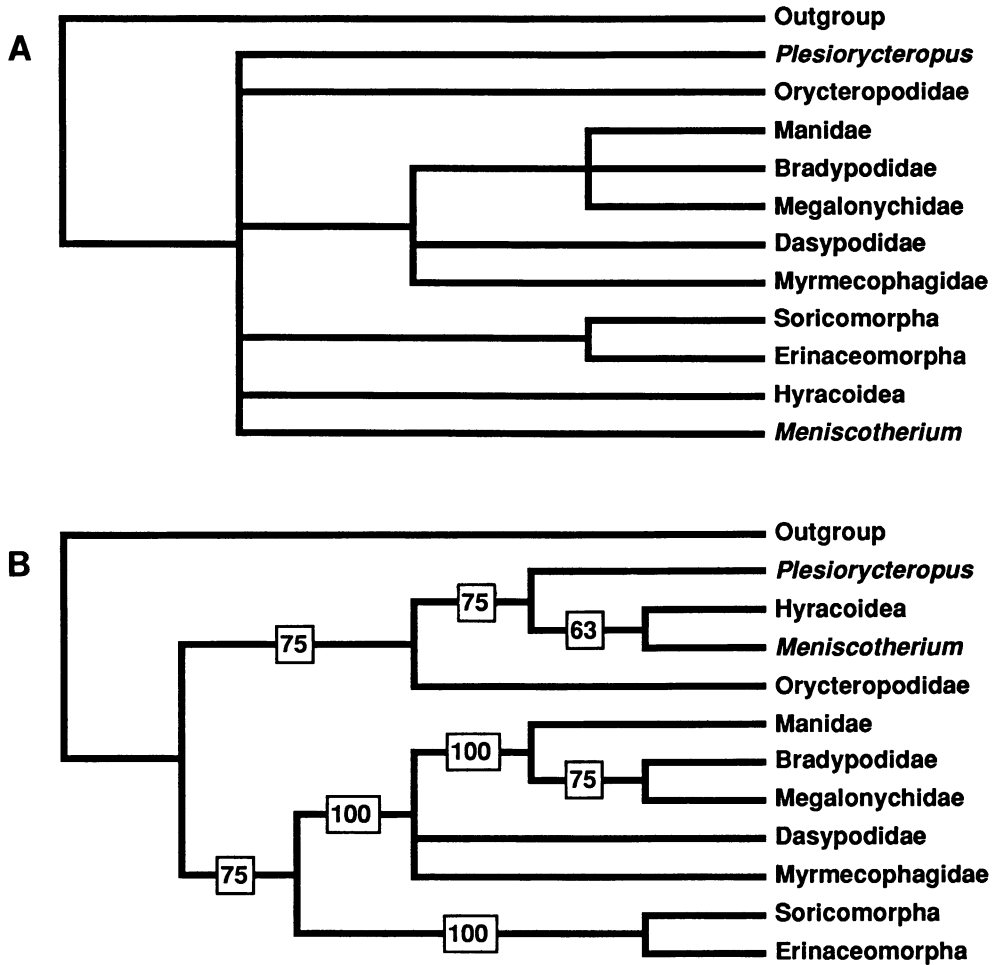


Fig. 52. Strict (A) and 50% majority-rule (B) consensus diagrams for eight MPTs derived from parsimony analysis of 32CM (table 18), all condylarthran taxa except *Meniscotherium* excluded (TL = 75, CI = 0.48, RI = 0.58; branch-and-bound routine). Resolution is much poorer than in figure 51, run with the 30CM. In cladogram B, figures on stems indicate proportion of all MPTs in which particular branches occur.

Novacek, 1989, 1992a) that tubulidentates + lipotyphlans form a distinct clade of eutherians (a grouping that, as of this writing, is nameless). Into this assemblage I force *Plesiorycteropus*, as the sister group of Tubulidentata. The remaining constraint stipulates that *Meniscotherium*, Hyracoidea, and *Plesiorycteropus* constitute a monophyletic group (ungulates, for lack of a better label). Results of a parallel set of runs, in this case using the 32CM to evaluate the influence of Patterson characters, are presented in table 25. The 32CM base run produced 8 MPTs; the strict consensus tree (fig. 52) displays much less

structure under the influence of Patterson characters.

General results for Group B runs are as follows:

(1) The ungulate constraint was satisfied within the group of MPTs in the 30CM and 32CM base runs (figs. 51, 52; tables 24, 25), and therefore entails no cost in terms of greater tree length.

(2) Trees compatible with the edentate constraint show up at +3 steps in the run with no Patterson characters (table 24) and at +2 steps in the run in which Patterson characters were utilized (table 25). Interestingly, in both

TABLE 23
Complete List of Apomorphies by Stems, Figure 51A^{a,b}

Stem	Character	CI	Change (→)		Optimi- zation
PLESIORYCTEROPUS	1. OPTC CANAL	0.5	0	1	
	6. NASL EXPAN	0.5	0	1	
	9. PTERY TYMP	0.5	0	1	
	*14. EPITYMP SIN	0.3	1	0	A
	16. FOR STAPED	0.5	0	1	
	19. TRNARC CAN	0.3	0	1	D
	20. HUMRL HED	0.5	0	1	
	21. RAD ULN PR	0.3	0	1	
	22. PUBIC SYMP	0.5	0	1	
	24. ISCH LAT PR	0.5	0	1	D
	25. ISCH EXPAN	0.5	0	1	
	29. ASTRAG PMP	0.5	0	1	D
	*30. UNGL PHAL	0.5	1	0	A
	+31. MAN REDUC	0.3	0	1	
	+32. ZYGO ARCH	0.3	0	1	
ORYCTEROPODIDAE	10. CAUD PR PET	0.5	0	1	
	14. EPITYMP SIN	0.3	0	1	D
	19. TRNARC CAN	0.3	0	1	D
	24. ISCH LAT PR	0.5	0	1	D
	30. UNGL PHAL	0.5	0	1	D
HYRACOIDEA	4. LACRML FAC	0.3	0	1	
	12. MAST EXPOS	0.5	0	1	
	16. FOR STAPED	0.5	0	2	
	17. INT CAR POS	1.0	0	2	
	*29. ASTRAG PMP	0.5	1	0	A
MENISCOTHERIUM	10. CAUD PR PET	0.5	0	1	
	*15. SUBARC FOS	0.3	1	0	
	29. ASTRAG PMP	0.5	0	1	D
MANIDAE	*2. INTPARIETL	0.5	1	0	
	13. PERCRN CAN	0.3	0	1	
	*18. XENARTHY	0.5	1	0	
	20. HUMRL HED	0.5	0	1	D
	*23. SACROISCH F	0.5	1	0	
	+31. MAN REDUC	0.3	0	1	
BRADYPODIDAE	*3. ALISPH-PAR	0.5	1	0	
DASYPODIDAE	6. NASL EXPAN	0.5	0	1	
	11. TEGMN SIZE	0.3	0	1	
	*20. HUMRL HED	0.5	1	0	A
	25. ISCH EXPAN	0.5	0	1	
	27. FEMUR HED	0.7	0	1	D
	*+32. ZYGO ARCH	0.3	1	0	A
MYRMECOPHAGIDAE	7. FOR ROTUND	0.3	0	1	
	20. HUMRL HED	0.5	0	1	D
	+31. MAD REDUC	0.3	0	1	
	+32. ZYGO ARCH	0.3	0	1	D
SORICOMORPHA	19. TRNARC CAN	0.3	0	1	
	21. RAD ULN PR	0.3	0	1	
ERINACEOMORPHA	11. TEGMN SIZE	0.3	0	1	
	16. FOR STAPED	0.5	0	1	

TABLE 23—(Continued)

Stem	Character	CI	Change (→)		Optimi- zation
STEM 1	13. PERCRN CAN	0.3	0	1	
	14. EPITYMP SIN	0.3	0	1	D
	*19. TRNARC CAN	0.3	1	0	A
	*24. ISCH LAT PR	0.5	1	0	A
	30. UNGL PHAL	0.5	0	1	D
STEM 2	5. LACRML FOR	1.0	0	1	
	7. FOR ROTUND	0.3	0	1	
	11. TEGMN SIZE	0.3	0	1	
	26. LESS TROCH	1.0	0	1	
	28. ASTRAG CTY	1.0	0	1	D
STEM 3	14. EPITYMP SIN	0.3	0	1	A
	15. SUBARC FOS	0.3	0	1	D
	19. TRNARC CAN	0.3	0	1	A
	24. ISCH LAT PR	0.5	0	1	A
	27. FEMUR HED	0.7	0	1	
	28. ASTRAG CTY	1.0	0	1	A
	29. ASTRAG PMP	0.5	0	1	A
	30. UNGL PHAL	0.5	0	1	A
STEM 4	7. FOR ROTUND	0.3	0	1	
	{ 20. HUMRL HED	0.5	0	2	D
	{ 20. HUMRL HED	0.5	1	2	A
STEM 5	4. LACRML FAC	0.3	0	1	
	14. EPITYMP SIN	0.3	0	1	D
	21. RAD ULN PR	0.3	0	1	
	{ 27. FEMUR HED	0.7	1	2	A
	{ 27. FEMUR HED	0.7	0	2	D
	+32. ZYGO ARCH	0.3	0	1	D
STEM 6	3. ALISPH-PAR	0.5	0	1	
	14. EPITYMP SIN	0.3	0	1	A
	15. SUBARC FOS	0.3	0	1	D
	17. INT CAR POS	1.0	0	1	
	27. FEMUR HED	0.7	0	1	A
STEM 7	2. INTPARIETL	0.5	0	1	
	8. FRON-PAR P	1.0	0	1	
	12. MAST EXPOS	0.5	0	1	
	16. FOR STAPED	0.5	0	2	
	18. XENARTHRY	0.5	0	1	
	20. HUMRL HED	0.5	0	1	A
	23. SACROISCH F	0.5	0	1	
	+32. ZYGO ARCH	0.3	0	1	A
STEM 8	1. OPTC CANAL	0.5	0	1	
	4. LACRML FAC	0.3	0	1	
	13. PERCRN CAN	0.3	0	1	
	*15. SUBARC FOS	0.3	1	0	A
STEM 9	9. PTERY TYMP	0.5	0	1	
	22. PUBIC SYMP	0.5	0	1	

^a Key: A, acctran; D, deltran; *, reversal; +, Patterson character.

^b Figure 51B differs only in that stem 1' (supporting *Plesiorhycteropus* + *Meniscotherium*) is defined by a single unequivocally placed transformation, C 29 (CI = 1.0). Stem 2' is identical to stem 2 except for presence of an extra transformation (C 13, to derived state), in acctran only.

TABLE 24
Effect of Topological Constraints on Most Parsimonious Resolutions of 30CM^a

	No constraint ^b	Ungulate constraint	Aardvark/ insectivore constraint ^c	*Edentata constraint	Xenarthran constraint
Steps	69 (2 MPTs)	[69]	73 ^b	72	75
CI	0.493	[0.493]	0.466	0.472	0.453
RI	0.593	[0.593]	0.547	0.558	0.523
Constraint cost (in steps)	—	+0	+4	+3	+6

^a Constraint statements:

Ungulate	((<i>Meniscotherium</i> , Hyracoidea, <i>Plesiorcyteropus</i>));
Aardvark/insectivore	((((Orycteropodidae, <i>Plesiorcyteropus</i>), Erinaceomorpha, Soricomorpha));
*Edentata	(((((Bradypodidae, Megalonychidae, Myrmecophagidae), Dasypodidae), Manidae), <i>Plesiorcyteropus</i>));
Xenarthran	(((((Bradypodidae, Megalonychidae, Myrmecophagidae), Dasypodidae), <i>Plesiorcyteropus</i>))

^b See figure 51.
^c The statement ((Orycteropodidae, *Plesiorcyteropus*)) appears at 71 steps (+2).

tables the edentate constraint is less expensive in terms of tree length than is the xenarthran one (+6 and +5 steps, respectively). The dyad Manidae + *Plesiorcyteropus*, not listed in these tables, is found at +5 and +2 steps, respectively.

(3) Satisfaction of the aardvark/insectivore constraint does not occur until +4 steps in either run. On the other hand, the less restrictive dyad *Plesiorcyteropus* + Orycteropodidae (i.e., without regard to the position of the insectivores) occurs at +2 steps in both runs.

Features of apomorphy distribution for one of the two MPTs generated from the 30CM (fig. 51A) are as follows (table 23):

(1) Stem 3, supporting *Plesiorcyteropus*,

Hyracoidea, *Meniscotherium*, and Orycteropodidae, is supported by only one unambiguously placed derived character, fovea interrupts margin of femoral head (C 27). This transformation occurs convergently in *Edentata (Dasypodidae/stem 6). Several ambiguously placed characters also support this stem. The strongest of these is the cotylar fossa of the astragalus (C 28), unique to this clade, which places on this stem in acctran but on stem 2 in deltran.

(2) As portrayed on stem 2 of this cladogram, *Plesiorcyteropus* and its sister group Hyracoidea + *Meniscotherium* form a separate clade, a grouping that is strongly supported by four unambiguously placed characters (C 5, 7, 11, 26). Both the extraorbital position

TABLE 25
Effect of Topological Constraints on Most Parsimonious Resolutions of 32CM^a

	No constraint	Ungulate constraint	Aardvark/ insectivore constraint ^b	*Edentata constraint	Xenarthran constraint
Steps	75 (8 MPTs)	[75]	79	77	80
CI	0.480	[0.480]	0.456	0.468	0.450
RI	0.576	[0.576]	0.533	0.554	0.522
Constraint cost (in steps)	—	+0	+4	+2	+5

^a Constraint statements: See table 24.
^b The statement ((Orycteropodidae, *Plesiorcyteropus*)) appears at 77 steps (+2).

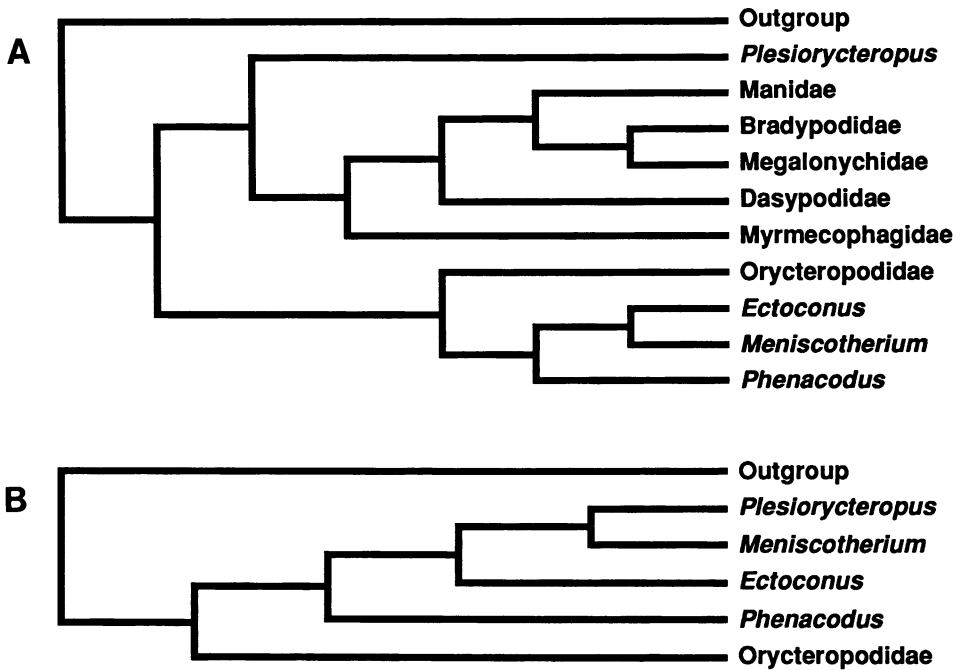


Fig. 53. Results when taxon list is restricted to conform with Patterson's (1975) comparisons. **A**, A single MPT is recovered with the taxon list restricted as seen here. Topologies are identical whether Patterson characters (C 31, 32) are used or not (included, TL = 63, CI = 0.55, RI = 0.65; excluded, TL = 58, CI = 0.56, RI = 0.66). Character support for *Plesiorcyteropus* + *Edentata includes unambiguously placed transformations C 9, 20, 22, and 32 (if Patterson characters included). **B**, A single MPT is also recovered if the taxon list is further restricted by omitting edentates (Patterson characters included, TL = 32, CI = 0.64, RI = 0.47; excluded, TL = 30, CI = 0.64, RI = 0.47).

of the lacrimal foramen and the flared, excavated form of the lesser trochanter are unique and unreversed. The other two (separate foramen rotundum, large tegmental size) are involved in convergences with other taxa in the cladogram. This clade is further bolstered by C 28 in the deltran character distribution.

(3) Stem 1, Hyracoidea + *Meniscotherium*, is unambiguously supported by loss of the percranial canal (C 13) and four ambiguously placed characters (C 14, 19, 24, 30), two of which involve reversions to the primitive state.

(4) The grouping of *Edentata and Lipotyphla as sisters is mandated by the gain of the tympanic process of the pterygoid/basisphenoid (C 9) and reduction of the pubic symphysis (C 22). Both transformations occur convergently in *Plesiorcyteropus*. As previously noted, relationships within the *Edentata assemblage as depicted in this

cladogram are unconvincing. Among other problems, both xenarthry (C 18) and innominate-sacral fusions (C 23), unambiguously placed on stem 7, have to undergo reversal to the primitive condition in Manidae. Also, the admittedly polyphyletic grouping of pholidotes and sloths is supported by only two unambiguously placed characters, lacrimal reduction (C 4) and radius-ulna proportion (C 21) on stem 5.

Character distributions in the second cladogram (fig. 51B) are slightly different. However, the grouping *Plesiorcyteropus* + *Meniscotherium* + Hyracoidea has the same support as in the first cladogram (C 5, 7, 11, 26).

GROUP C RUNS: TUBULIDENTATE AND EDENTATE HYPOTHESES RECONSIDERED

It is objectionable to vary the content of a taxon or character list merely in order to move

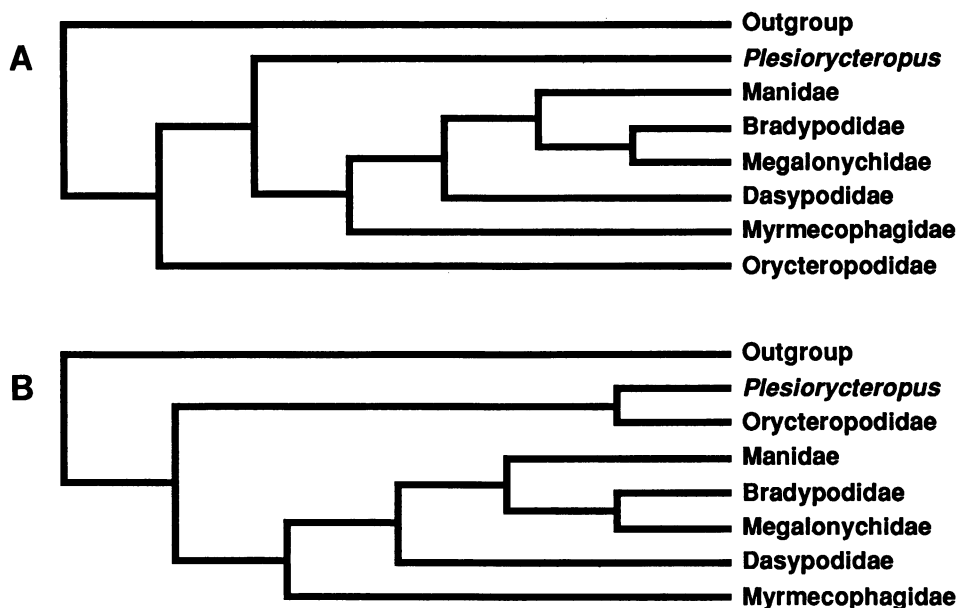


Fig. 54. Results when taxon list is restricted to conform with Lamberton's (1946) comparisons. **A**, If Patterson characters and all condylarthrans, hyracoids, and lipotyphlans are omitted from the parsimony analysis, in the single MPT (TL = 48, CI = 0.65, RI = 0.64) recovered from the parsimony analysis *Plesiorcyteropus* groups with edentates. **B**, If polymorphism in C 28 and 29 in Orycteropodidae is ignored (table 18) and it is assumed that the derived state obtains for both characters in aardvarks, a single MPT (TL = 49, CI = 0.64, RI = 0.64) is recovered in which *Plesiorcyteropus* now groups with Orycteropodidae to the exclusion of edentates.

a target taxon to a more favored position on an MPT. However, it is of some interest to examine how the hypotheses framed by Lamberton (1946) and Patterson (1975) fare when the present character analysis is run against only those taxa specifically considered by the authors in question.

Patterson (1975) essentially restricted his comparisons to Orycteropodidae, Xenarthra, Manidae, and condylarthrans. Analyzing only these groups and *Plesiorcyteropus*, we find that only 1 MPT is recovered whether Patterson characters are included or not (fig. 53A): *Plesiorcyteropus* groups with *Edentata, while Orycteropodidae groups with condylarthrans. In figure 53B, the taxon list is restricted to some condylarthrans, Orycteropodidae, and *Plesiorcyteropus*; in this case, the Malagasy taxon pairs with *Meniscotherium*. Little should be made of these results, because other combinations of taxa yield different topologies. However, it seems reasonable to conclude that Patterson's endorsement of a close relationship between

Plesiorcyteropus and Orycteropodidae is not supported by the character evidence considered here, even when the taxon list is restricted to conform to his set of comparisons.

With respect to Lamberton's hypothesis, the 30CM yields 1 MPT if ungulates and lipotyphlans are excluded and comparisons are thereby restricted to xenarthrans and manids (fig. 54A). The topology of the MPT is the same whether or not Patterson characters are included (*Plesiorcyteropus* groups with *Edentata, from which Orycteropodidae is excluded). The stability of this result is not great, however. For example, if we ignore polymorphism in C 28 and 29 (due to retention of primitive states in *Myorycteropus*) and score Orycteropodidae as derived for both characters, parsimony analysis of the 30CM data matrix again yields 1 MPT (fig. 54B). This time the sister group of *Plesiorcyteropus* is Orycteropodidae and edentates are relegated to a separate arm. (With the 32CM, Orycteropodidae is the sister group in 3 out of 4 MPTs.) One's conclusion from this ex-

ercise is that outcomes will be highly dependent on which taxa one considers worth comparing and how the character list is restricted.

ANALYTICAL RESULTS USING NOVACEK'S 88-CHARACTER MATRIX

There are only a handful of morphology-based cladistic treatments of higher-level eutherian systematics, and none of these considers *Plesiorcycteropus*. However, it is of great interest to see how this taxon performs when interpolated into an analysis that uses a different character set and taxon list. The data matrix I use for this purpose is the most recent published version of Novacek's 88-character matrix (cf. Novacek, 1989, 1992a).

I have made six changes to the 88CM. The first emendation affects character 31, "subarcuate fossa very shallow or absent." This was judged to be a derived trait by Novacek and Wyss (1986a), and was therefore correctly identified as an apomorphy of Tubulidentata in this and subsequent papers by Novacek and co-workers. However, the derived state was inadvertently changed to "0" in the aardvark row of the data matrix as published, an error that I now correct.

The other emendations concern appropriate scoring, for Pholidota, of dental characters 11, 12, 20, 54, and 58. These changes make no difference to computed tree length or recovered topologies, but they do make an epistemological difference. The rigid empiricist stance, followed here, is that character states can be assessed if and only if the relevant anatomical entity is represented in the OTU. Therefore, because pholidotes lack dental structures, any character requiring an actual assessment of tooth morphology should be left unrated (i.e., as "9"). The rule is not abrogated in the case of character 29, because this character concerns tooth *suppression*. The difference is that the desideratum for this character is detection of an absence, perfectly acceptable in this instance because of the way in which the character is framed. For the dental characters, however, the desiderata are physical qualities inherent to teeth; these cannot be detected unless the teeth themselves physically exist and can be studied.

I recognize that arguments exist for "parsimoniously" forcing character state deci-

sions in the absence of any anatomy to support them, and in other contexts I have used such arguments myself (e.g., to argue for the presence of petrosal-derived bullae in early Tertiary primates of modern aspect; MacPhee et al., 1983). However, the place to make all such inferences is *after* cladistic analysis has been undertaken, not before. For example, I know of no empirical procedure that would permit me to verify that edentulous Pholidota displays the derived state, "upper molars (primitively) with narrow stylar shelves" (character 20 of Novacek, 1989, 1992a). It is one thing to infer this apomorphy for the ancestry of Pholidota from parsimony considerations (all dentulous eutherians code as "1" in the 88CM); it is quite another to input it into a data matrix *as though it were empirically verifiable*.

Analysis of the corrected 88CM using the branch-and-bound algorithm in the PAUP 3.0s package produces 4 MPTs of 112 steps each (CI = 0.77, excluding uninformative characters; RI = 0.84). The earlier version produced 10 MPTs of 111 steps (CI = 0.78). Additional runs with and without the character alterations made above prove that the extra step is exclusively due to the change made to character 31 in the Tubulidentata row. Despite the extra step, none of the conclusions made by Novacek (1989) regarding the consistency of certain groupings (or lack thereof) is materially affected. Major clades retain their content (and their basal instability), and the strict and Adams consensus trees are identical to each other and to the consensus tree published by Novacek (1989).

Adding *Plesiorcycteropus* to the taxon list presents problems of data completeness, nearly inevitable for fossil material. This topic has been explored in relation to fossils by Novacek (1989, 1992a), who examined the effect on cladistic resolution when fossil taxa are added to the 88CM. He found that on recovered cladograms, fossil taxa tended to be markedly unstable in their assignments, although a few placed rather consistently next to certain groups. Novacek argued from the latter observation that the proportion of missing data for a given fossil taxon was not necessarily a good predictor of the scale of its instability among several equally parsimonious topologies. I extend this inquiry here

TABLE 26
Assumption Sets for Novacek's 88CM^a

Assumption set:	0 (minimum)	1 (*Edentata)	2 (Tubulid.)	3 (Ungulata)	Omitted CS
Matrix:	9999199990	9999199990	9999199990	9999199990	9999199990
	9909999919	9909999919	9909999919	9909999919	9909999919
	9999191999	9999191919	9999191919	9999191999	9999191999
	1091009099	1091009099	1091009099	1091009099	1091009099
	0009099999	0009099999	0009099999	0009099999	0009099999
	9009999900	9009999900	9009999900	9009999900	9009999900
	9999090900	9999090910	9999090900	9999090900	9999090900
	9909909090	9909909090	9909909090	9909909090	9909909090
	00000990	00000990	00000911	00000910	000009
Changes:		#29: 9 → 1	#29: 9 → 1	#87: 9 → 1	#87, 88: → 8
(compared to set 0)		#69: 0 → 1	#87: 9 → 1		
			#88: 0 → 1		

^a In each column, character states are in the same order as in Novacek's (1992a) data matrix (characters 1–88), beginning with first entry in upper left of each column and ending with last entry in lower right.

by examining the appropriateness of making guesses to “improve” the data base for fossil OTUs, using *Plesiorhycteropus* as my example. Results demonstrate that making guesses about absent, poorly preserved, or otherwise ambiguous morphology, even for a small number of characters, tends to cause severe deformations in cladistic solutions.

Tables 26 and 27 present variant data lines (“assumption sets”) for *Plesiorhycteropus* and results of five PAUP runs in which these variant data were used. In set 0 (extreme left-hand column, table 26), any feature not verifiably represented in the existing hypodigm of *Plesiorhycteropus* was left unrated (“9”), and consequently there are no assessments of characters whose empirical referents are soft tissues, teeth, jaws, carpal elements, and so forth. Nor are there evaluations of characters whose referents on existing specimens are broken or otherwise damaged to such a degree that a rigorous empiricist might conclude that their states cannot be unambiguously resolved. In the subsequent three runs, this strong criterion is waived in the case of a small number of “swing” characters that, for various legitimate reasons, might be evaluated in different ways by different observers. The characters in question are characters 29 (tooth suppression), 69 (pelvic fusion), 87 (glaserian fissure condition), and 88 (tympanohyal condition). Physical evidence for the swing characters is defective in one way

or another, although if extrinsic considerations (assumed phylogenies, nature of fossil recovery) are allowed to play a role, it may be argued that there is enough information to permit informed guesses about applicable character states. Character 69 will be familiar, as it is equivalent to the derived state of character 23 in the 30CM (although differently scored). Character 29 is roughly equivalent to the derived state of character 31 in the 32CM, while the remaining two characters were not used in my runs (see Rejected Characters). Some other characters could have been treated as swing characters as well (e.g., character 27, scored as derived on the basis of two of the three bibymalagasy skulls with partial orbital regions), but this would not materially affect the results presented below. While I never manipulated more than 1.0–3.5% of the 88-character matrix for any single run, very different series of MPTs were generated depending on the assumption set used.

Assumption set 0 (Minimum). There is only a small number of derived characters in the 88CM that can be unambiguously scored as “1” for *Plesiorhycteropus* (table 26: characters 5, 19, 25, 27, 31, and 34). Bibymalagasy can be unambiguously, albeit unhelpfully, rated as “0” for an additional 28 characters, and as “9” for the remaining 54 characters. The resulting Nonambiguous Character Index (UCI) is 0.39 (table 27). It should be noted that this index is much lower than any re-

TABLE 27
Comparison of Five Runs Using Novacek's Revised 88-Character Set

Assumption set	TL ^a	MPT	CI	RI	UCI	NC	Sister-group arrangements in MPTs ^b			
							(P,T)	(P,E)	(P,U)	(P,O)
0 (minimum)	113	10	0.762	0.837	0.386	NA	—	4	2	4
1 (*Edentata)	113	4	0.762	0.837	0.398	2	—	4	—	—
2 (Tubulidentata)	113	4	0.762	0.837	0.409	3	4	—	—	—
3 (Ungulata)	114	31	0.755	0.829	0.398	1	4	4	2	21 ^c
Omitted CS	[109]	4	NA	NA	[0.384]	NA	—	4 ^d	—	—

^a Abbreviations: TL, tree length; MPT, no. of most parsimonious trees; CI, consistency index; RI, retention index; UCI, nonambiguous character index $([\text{total states} - "9\text{s}"] \div [\text{total states}])$; NC, maximum no. of changes in states (see table 26); P, *Plesiorcyteropus*, T, Tubulidentata, E, *Edentata (Xenarthra + Pholidota), U, Ungulata; O, other possibilities.

^b The last four columns are headed by sister-group statements (see abbreviations, footnote a); trees containing the relevant statement are placed under the appropriate column.

^c In this run, most "Other" sister-group relationships involving *Plesiorcyteropus* showed it as sister to Tubulidentata + Insectivora.

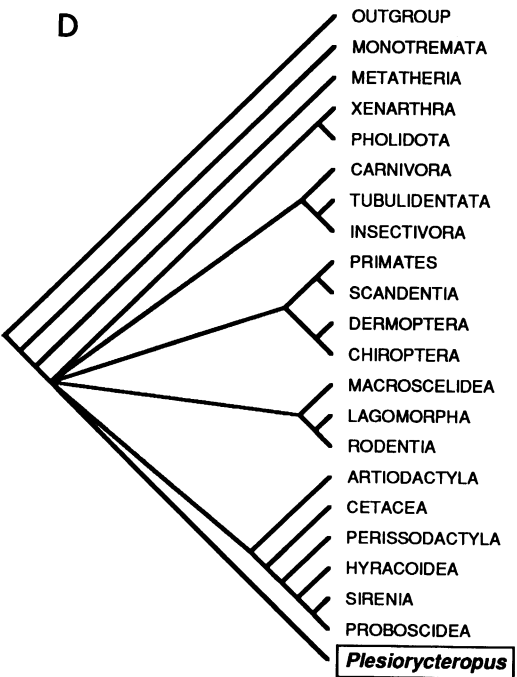
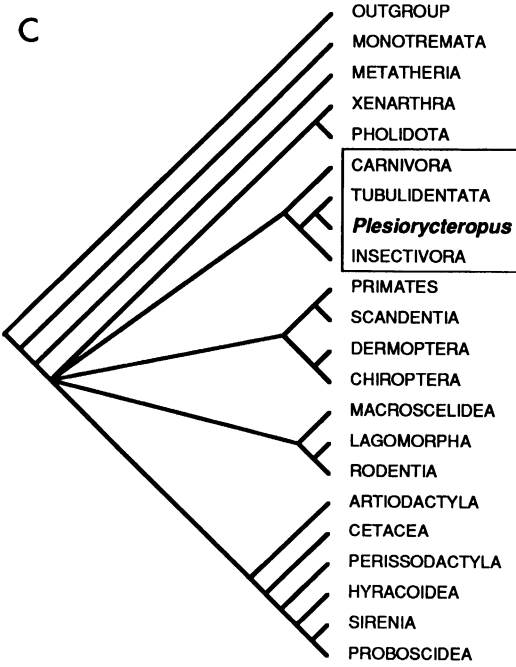
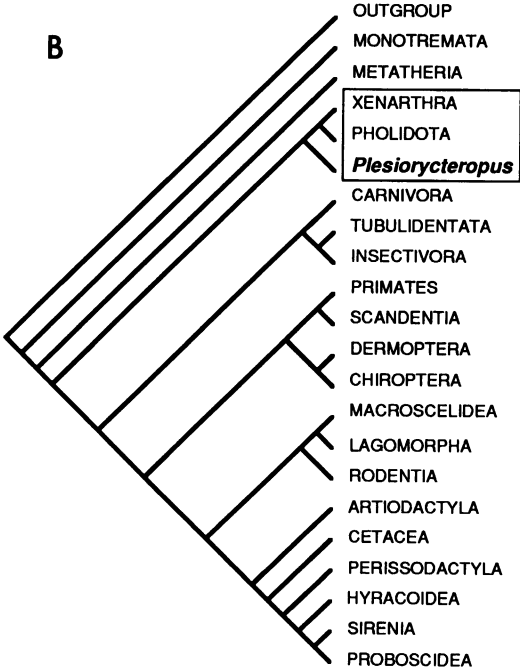
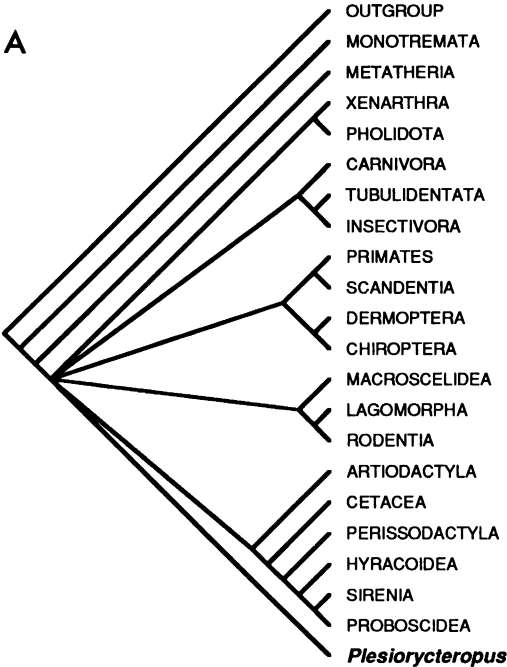
^d Outgroup to *Edentata + *Plesiorcyteropus* was always Tubulidentata.

ported by Novacek (1989), who did not consistently apply an equivalent of the physical referent rule (as is evident from his scoring of certain characters, e.g., character 39). Of the six derived characters of *Plesiorcyteropus* in this list, character 5 confirms that it is a therian, with characters 19 and 25 confirming more particularly that it is a eutherian—points not in contention here. More precise placement of *Plesiorcyteropus* within the eutherian ingroup is therefore completely dependent on the effect of characters 27, 31, and 34. In the interpretation of Novacek et al. (1988), character 27 is restricted to Xenarthra and Pholidota, while 34 is said to be present in all eutherians *except* the two just named. Character 31 is scattered without discernible pattern among eutherian orders and is regarded as being the "least stable" character in the analysis (Novacek and Wyss, 1986a).

Plesiorcyteropus found no consistent seating in the 10 MPTs generated in this run. In four of these trees, *Plesiorcyteropus* paired with Xenarthra/Pholidota; in two it was sister to all of Ungulata; and in one, to all of Epitheria. In the remainder it was diversely positioned, but never in close proximity to Tubulidentata. In the strict consensus diagram (fig. 55A), the eutherian "basal bush" is a 6-tomy and *Plesiorcyteropus* is on its own emergent, signifying that its relationships within Eutheria are completely unresolved.

*Assumption set 1 (*Edentata)*. In this set, the UCI is marginally better at 0.40, the increase being due to the addition of tooth suppression (29) and pelvic fusion (69) to the pool of derived characters. The extrinsic evidence for character 29 is the paleontological failure to recover either teeth or jaws attributable to bibymalagasy, a point explored at length in the Introduction. The extrinsic evidence for character 69 is seriously impugnable (see Characters and Transformations). For present purposes, it suffices to assert that, if pholidotans and xenarthrans can be said to be the "same" for this character (fide Novacek and Wyss, 1986a), then by the same token so can *Plesiorcyteropus*. These maneuvers increase the derived-state count for *Plesiorcyteropus* to 8; primitive states drop to 27 and ambiguous states to 53, for an overall change of 2.

The basic statistics for this run are identical to those for assumption set 0. However, this time only 4 MPTs were recovered, and 100% of them include an exclusive sister-group relationship between *Plesiorcyteropus* and Xenarthra/Pholidota. I also ran the matrix with character 69 altered but character 29 left unchanged. Output was precisely the same, except that now character 69 is shared by Xenarthra + Pholidota only, instead of by an inclusive *Edentata + *Plesiorcyteropus*. Tree statistics, not reported here, changed



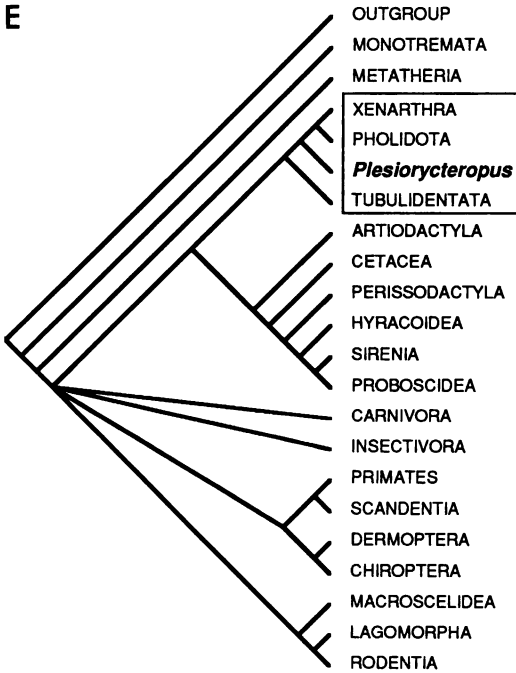


Fig. 55. Strict consensus diagrams of trees derived from revised version of Novacek's 88-character matrix (cf. Novacek, 1989, 1992) and generated under different assumption sets (see text and tables 26 and 27). **A**, Assumption set 0 (no bias, no character alterations); position of *Plesiorhycteropus* on the eutherian cladogram is completely unresolved. **B**, Assumption set 1 (*Edentata bias, 2 character alterations); *Plesiorhycteropus* groups as sister taxon to Xenarthra + Pholidota. **C**, Assumption set 2 (Tubulidentata bias; 3 character alterations); *Plesiorhycteropus* groups as sister to Tubulidentata within a clade that also contains Insectivora and Carnivora. **D**, Assumption set 3 (Ungulata bias, 1 character alteration); identical to diagram for assumption set 0, except that in this run 31 MPTs were recovered, +1 step longer (114 vs. 113). **E**, Characters 87 and 88 of original matrix deleted; *Plesiorhycteropus* groups with Xenarthra, Pholidota, and Tubulidentata (forming classic Cuvierian *Edentata). Adams consensus diagrams were computed for all five runs; in each case, diagrams were individually identical to their strict consensus counterparts.

miniscule (e.g., retention index dropped from 0.837 to 0.836). Apparently, with this data set, in order to have *Plesiorhycteropus* consistently group with *Edentata, an assertion of edentulousness suffices. In the strict consensus tree (fig. 55B), the eutherian basal

bush is pectinate and *Plesiorhycteropus* is now attached to the edentate branch. In the usual logic of these things, this outcome could be said to be an improved resolution of relationships compared to those delivered by assumption set 0.

Assumption set 2 (Tubulidentata). Bias in favor of aardvarks permitted three character state changes compared to assumption set 0. Character 29 was retained with the change introduced in assumption set 1 (fide Novacek and Wyss, 1986a). Although the tympanic floor is incomplete on all skulls of *Plesiorhycteropus*, it could have possessed the derived condition of the glaserian fissure (87) defined by Novacek (1989) for Tubulidentata. The tympanohyal (88) is not elongated in available skulls, but it is "large," and if the descriptor "nearly touches the promontorium" is liberally interpreted, the condition seen in *Plesiorhycteropus* might also be described by an observer as like that of tubulidentates.

TL, CI, and RI were identical to values seen in the first two runs, and the Nonambiguous Character Index was trivially higher (0.41). Four MPTs were recovered, as in the previous run. However, with respect to the identity of nearest neighbors, results were completely different: in this run, all MPTs allied *Plesiorhycteropus* and Tubulidentata as sister taxa, in a clade that also incorporated carnivores and insectivores but no edentates. The strict consensus (fig. 55C) featured the same 4-member clade, whose stem formed one emergent from a basal 5-tomy.

Two variants were also run. In both, the change to character 29 was retained. In the first variant, character 88 was altered but character 87 was left in its original state; in the second variant, the converse treatment was applied. In the first variant exactly the same results were achieved as in the main run for this bias set, and character 87 remained a synapomorphy of the Insectivora/Tubulidentata/*Plesiorhycteropus* clade. By contrast, running the second variant resulted in 8 MPTs of 114 steps (CI = 0.76). The eight trees were evenly divided in their resolution of the sister taxon of *Plesiorhycteropus* (four each for Tubulidentata and *Edentata). The consensus tree, an 8-tomy, was much less resolved because Insectivora and Carnivora were situated on their own emergents.

Assumption set 3 (Ungulata). In this set, only 1 character (87) was altered compared to the minimum assumption set. The strict consensus diagram (fig. 55D) is identical to the one recovered for assumption set 0, but the TL is longer by +1 step and the number of MPTs is greater (31 trees). Of these trees, the bias-favored outcome—an exclusive sister-group relationship of *Plesiorhycteropus* and the ungulate orders—was found in only 6% of all trees. The two outcomes favored in preceding runs were represented in 12% of all trees each, while “other” solutions accounted for the rest. Interestingly, the majority of “other” solutions—16/31, or 52% of all trees—contained a clade in which *Plesiorhycteropus* was sister to Tubulidentata + Insectivora. This clade did not occur in a single MPT generated in any other run, the closest approximation being the grouping in which Insectivora is sister to Tubulidentata + *Plesiorhycteropus* (cf. discussion of assumption set 0).

Which, if any, of these results ought to be taken as the “best” resolution of the placement of *Plesiorhycteropus*? One might be tempted to place some meaning on the frequency with which certain solutions appear, whatever the assumption set (e.g., *Plesiorhycteropus* + *Edentata). To me, however, the large number of “other” solutions in these runs implies that the 88-character matrix may not contain enough information to provide for the reliable placement of underdetermined groups like bibymalagasy. Even the smallest manipulations disrupt patterns, as may now be appreciated from a different direction, character deletion.

Omitted Characters. In this final run, characters 87 and 88 of the original matrix were deleted (for justification, see Rejected Characters). The reduced character matrix yielded 4 MPTs under assumption set 0. The two deletions strongly affected some associations. Insectivora showed no consistency in its attachments to other branches, while Tubulidentata joined the Xenarthra/Pholidota clade in every case. So did *Plesiorhycteropus*—the net effect being to reconstitute a Cuvierian version of *Edentata in the strict consensus diagram (fig. 55E) in just the way that Lambertson envisaged it!

DISCUSSION

Do any of the parsimony analyses examined in the two preceding sections provide a suitable basis for assessing the cladistic position of *Plesiorhycteropus*? Overall, the prospects are not good. Most supraordinal assemblages, not robustly defined for Eutheria in any case, offer little in the way of simplifying assumptions. With respect to the runs made using Novacek's 88CM, bibymalagasy could be either an edentate, or an epithere, or neither, depending on how certain characters are scored. Clearly, the information content of the bibymalagasy hypodigm is simply inadequate to permit a reliable placement using Novacek's system of characters. This observation does not apply in the same way to the 30CM, since it was possible to score *Plesiorhycteropus* for every character analyzed. However, in actuality this made little difference to the outcome, because the cladistic position assumed by *Plesiorhycteropus* varied significantly among runs. Much of the variation appears to be due to which taxa are left in or out of the parsimony analysis—a bad sign. A similar problem is presented by the exclusion or modification of specific character states (see Analytical Results Using Novacek's 88CM).

In the most taxically inclusive run in Group A, the dyad *Plesiorhycteropus* + Orycteropodidae is found in 100% of recovered trees, but the identity of the next outgroup (Hyracoidea or *Meniscotherium*) is unresolved (fig. 48). This area of instability might seem unimportant, given the apparently solidity of the primary result. However, it can be shown that the condylarthran taxa have a decided effect on topology, particularly with respect to the fine positioning of Hyracoidea vis-à-vis Orycteropodidae. If all fossils are deleted, Hyracoidea is preferred over Orycteropodidae as the sister taxon of *Plesiorhycteropus* (fig. 50). Echoing this point, the Group B runs (fig. 51, table 24) reveal that it is always more parsimonious to refer *Plesiorhycteropus* to a general ungulate grouping that includes Hyracoidea than to an exclusive pairing with Orycteropodidae.

Admitting that parsimony analysis is inconclusive with respect to the identity of the

sister group of *Plesiorhycteropus*, can it nevertheless be used to say something about what *Plesiorhycteropus* is probably *not* closely related to? On the basis of Group B runs (tables 24, 25), it appears to be considerably more expensive, in terms of tree length, to unite *Plesiorhycteropus* with either Xenarthra or Xenarthra + Pholidota than with ungulates. But in Group C runs (figs. 53, 54), *Plesiorhycteropus* preferentially joins Xenarthra + Pholidota and cannot be made to group exclusively with *Orycteropus* unless the data are manipulated.

Lipotyphlans fail to group with *Plesiorhycteropus* in any of the manipulations reported here. In one Group A run (no fossils, 30CM) not discussed in the preceding section, Erinaceomorpha was removed from the taxon list. The single MPT produced by the parsimony analysis of character distributions of the remaining taxa represented *Plesiorhycteropus* and Soricomorpha as sister taxa (which were, in turn, sister to edentates). The character support for this dyad (C 1, 19, and 21) is no thinner than it is for most other solutions reported here, although this result would probably be regarded as one of the least compelling.

Accepting that the limits of resolution of the parsimony analyses have now been reached and do not permit any decisive conclusions, is there anything to indicate where we might look for future illumination concerning the cladistic position of *Plesiorhycteropus*? It will not have been lost on the reader that Ungulata, defined so as to include aardvarks, hyracoids, and condylarthrans, contains all of the non-edentate taxa considered here to which *Plesiorhycteropus* shows meaningful resemblances. Describing bibymalagasy as being a little like aardvarks and a little like hyraxes strikes a minor historical chord, because Le Gros Clark and Sonntag (1926) framed the hypothesis that hyracoids and tubulidentates are related in some phylogenetically significant way. This theme is now being replayed by molecular systematists, although so far with little fanfare (e.g., Rainey et al., 1984; Sarich, 1993; see also McKenna, 1992).

Although there are several characters in the 30CM that consistently appear in the PAUP

runs on stems supporting various groupings of ungulates, the two most intriguing from the standpoint of higher-level relationships concern the astragalus (C 28, 29). Versions of the posteromedial process and cotylar fossa occur in graviportal elephantids, scansorial and arboreal procaviids, primitive quadrupedal tubulidentates, at least some condylarthrans, and, most intriguingly, in the functionally and phylogenetically enigmatic *Plesiorhycteropus*. The possible significance of this is worth brief exploration.

Tethythere/ungulate specialists are currently using very similar astragalar characters as candidate synapomorphies of groups of interest to them. For example, a large, jutting medial process of the astragalus has been cited as a strong character for uniting Proboscidea and a host of early Tertiary genera sometimes regarded as related to elephants or to sirenians (or to both; cf. Gingerich et al., 1990). Thus Tassy (1982) utilized presence of the posteromedial process (his tuberculum mediale) as a synapomorphy to join *Barytherium* and *Moeritherium* with Proboscidea, and Gingerich et al. (1990: 76) have used the same trait to affirm a proposed relationship between *Anthracobune* and tethytheres. (These latter authors explicitly classified *Anthracobune* as a proboscidean, but stated that this allocation "does not preclude Anthracobunidae from ancestry of aquatic Desmostylia and possibly also Sirenia.") On the astragali of at least some primitive proboscideans (e.g., *Palaeomastodon*, *Numidotherium* [Andrews, 1906; Mahboubi et al., 1986]), there is not only a posteromedial process but also a rounded facet for the medial malleolus—interpretable as a primitive cotylar fossa.

Rasmussen et al. (1990) considered the "deep, rounded articular fossa for the medial malleolus" of all known fossil and extant hyracoids to be "an exclusive similarity" to primitive proboscideans, echoing the similarity in the serial or taxopode organization of the tarsal bones in both groups. This point now appears in another light: *Orycteropus* slightly and *Plesiorhycteropus* emphatically deepen the cotylar fossa, and both present well-developed (if somewhat differently shaped) posteromedial processes. Broaden-

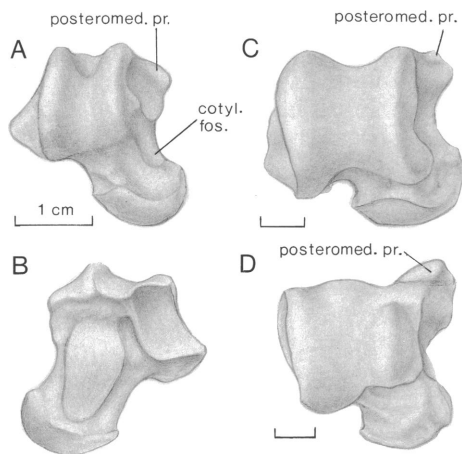


Fig. 56. Astragali of **A**, the Paleocene meniscotheriid *Meniscotherium* sp., dorsal view; **B**, same, ventral view; **C**, the extant ursid *Ursus americanus*, dorsal view; and **D**, the Quaternary caviomorph *Amblyrhiza inundata*, dorsal view. A posteromedial process is present in each taxon illustrated. *Meniscotherium* additionally possesses a small but definite cotylar fossa. All scales 1 cm.

ing the distributional base still further, it may be noted that S. McGehee (personal commun.) has found cotylar fossae in several South American ungulates reminiscent of the one described for *Meniscotherium* (C 28, 29; fig. 56A, B).

In *Orycteropus* but not *Plesiorycteropus*, the talocrural joint surface spreads onto the posteromedial process, suggesting that this latter structure acts as a pillar to provide additional support for the medial aspect of the leg. A similar function may be attributed to the posteromedial process of *Palaeomastodon* and *Numidotherium*, judging from illustrations presented by Mahboubi et al. (1986). Theissen and Domning (1992: 498) defined a taxon *Pantomesaxonia* that includes hyracoids, tethytheres, and perissodactyls but none of the condylarthran taxa they investigated. The only astragalar character quoted in support of *Pantomesaxonia* is absence of the astragalar canal, also absent in *Plesiorycteropus* but present in *Orycteropus*. (The only cranial synapomorphy of *Pantomesaxonia* with a high CI that can be checked on *Plesiorycteropus* is described as “foramen stylomastoid-eum primitivum close to vestibular window [character 30],” but in the appendix this char-

acter is defined as “foramen faciale [sensu MacPhee, 1981] well rostral to fenestra vestibuli.” The information content may be the same but the use of nonequivalent features in these definitions is confusing.)

While these astragalar features certainly deserve closer scrutiny as possible derived traits of a superordinal grouping that includes *Plesiorycteropus*, they occur in a few other mammals, which raises the problem of convergence. For example, a pronounced posteromedial process is found in *Ursus* and the extinct giant rodent *Amblyrhiza* (fig. 56C, D). In *Amblyrhiza* the malleolar facet per se is quite small and lacks a cotylar extension onto the astragalar neck. However, there is a lengthy posterior extension of the talocrural joint surface onto the posteromedial process (fig. 56D). Although the effect is not quite proboscidean, the design elements are the same, and it appears reasonable to assume that in *Amblyrhiza* the posteromedial process functioned as an ancillary platform for tibial support. Graviportal locomotion is the functional basis for convergence in this case, but not in others. For example, deep cotylar fossae occur in elephant shrews and a number of Old World monkeys (e.g., macaques).

The significance of these newly recognized astragalar characters will have to await additional evaluations, but more than any other series of attributes discussed here, they suggest that there is merit to the notion that *Plesiorycteropus* is an ungulate of some sort. If *Plesiorycteropus* were at present known only from its astragalus, I do not doubt that there would be much speculation in the literature to the effect that a hyrax relative, or primitive proboscidean, or possibly a condylarthran, had lived until recently in Madagascar. I am much less certain that anyone would have exclusively thought of armadillos in this regard.

CONCLUSION: A NEW ORDER OF EUTHERIAN MAMMALS

While a parsimony analysis will always provide *some* solution to a problem, it does not follow that any such solution has merit. None of the analyses conducted in the preceding section did much to lift the veil of ambiguity shrouding the phylogenetic rela-

tionships of *Plesiorcyteropus*, even at very high hierarchical levels within Eutheria. While it can always be maintained that the characters chosen to assess the relationships of *Plesiorcyteropus* in this study are inadequate in one way or another, it becomes increasingly difficult to accept such an argument when all pertinent facts have been considered. This I believe has been done in the morphological and analytical sections of this monograph, and it is therefore time to come to the conclusion that, in my estimation, is dictated by those facts: recognition of the distinctiveness of *Plesiorcyteropus* by the erection of a new higher taxon to receive it.

BIBYMALAGASIA, NEW ORDER

CONTENT: *Plesiorcyteropus*, only contained genus, from subRecent of Madagascar (now extinct). A few other taxa may deserve scrutiny if additional material comes to light (e.g., *Palaeorycteropus*, *Leptomanis* [see Appendix I]), but none of these is considered a likely member at present.

ETYMOLOGY: Name is a latinization of manufactured common name, "bibymalagasy" (see Introduction, Taxonomy). Names of animal taxa above the family-group level are not regulated by the ICZN (Art. 1[b][4]). Although it is a frequent practice to base higher-level names on some previously published name of generic rank by the addition of an appropriate suffix, this practice is not mandated except by convention. Where there is no historical convention, as in mammalogy, other considerations should be allowed to play a role, such as the internationalization of nomenclature through the use of names derived from appropriate vernaculars. I take advantage of this opportunity to use a distinctively Malagasy name for a uniquely Malagasy mammal.

DIAGNOSIS: Morphological features as for only contained genus, *Plesiorcyteropus* (see Introduction, Taxonomy), of which the following provide a differential diagnosis:

(1) Differs from all members of the comparative set except Tubulidentata and Lipotyphla in possessing transarcual canals in certain vertebral neural arches. Differs from known tubulidentates and possibly all lipotyphlans in the following combination of fea-

tures: canals occur in first sacral, lumbar, and posterior thoracic vertebrae; are large; and are perforating. (Transarcual canals may occur in some other eutherian groups, as detailed in table 10, but incidence and homologies presently uncertain.)

(2) Differs from all members of the comparative set except Tubulidentata, *Ectoconus*, and *Meniscotherium* in possessing a distinct posteromedial process of the astragalus. Differs from Tubulidentata, *Ectoconus*, and *Meniscotherium* in that the bibymalagasy posteromedial process has a distinct ventral groove for flexor tendons. (Posteromedial processes occasionally seen in other eutherians, and most frequently in certain ungulate groups; process may not be functionally or homologically equivalent in all taxa.)

(3) Differs from all members of the comparative set except Dasypoidea in possessing large ischial expansions. (Morphologically similar ischial expansions found in certain anthropoid primates and chalicotheriid perissodactyls; in primate examples expansions bear specialized sitting pads.)

DISCUSSION: Nearly all of the points that would ordinarily need to be made at this juncture are made at length elsewhere in this monograph, but there are certain objections to the systematic measures taken here that can be anticipated:

1. Separation of *Plesiorcyteropus* from Tubulidentata is not justified.

Although *Plesiorcyteropus* has been formally classified as a tubulidentate since its initial description in 1895, the character evidence that can be used to support this allocation is thin. The morphological evaluations presented in this monograph demonstrate that, although similarities to orcyteropodids certainly exist, so do resemblances to a wide variety of other taxa. Parsimony analysis of character distributions fails to show a preponderance of evidence favoring the continued incorporation of *Plesiorcyteropus* within Tubulidentata.

The inclusion of doubtfully related taxa within a monophyletic group merely complicates future systematic work, because the suspect forms will affect critical aspects of character analysis (e.g., evaluation of polymorphism, morphotype reconstruction, distributional evidence, etc.). It is important not

to take current enthusiasm for cladogenizing all of Mammalia to an unsupportable extreme: shorn of *Plesiorcyteropus*, Tubulidentata once again becomes a well-circumscribed group. Similar reasoning informs the decision by Thewissen and Domning (1992) to separate order Phenacodonta (Meniscotheriidae + Phenacodontidae) as a definable clade within the condylarthran dustbin.

2. Creation of a new order brings no corresponding illumination of relationships.

If the point of any program of systematic research is to detect *relationships*, then the erection of a monotypic order for *Plesiorcyteropus* without being able to define its sister group is a tacit admission of failure to complete the program. I recognize the validity of this position, but I also note that Bibymalagasia is scarcely unique in this regard: in my opinion, programs have yet to be completed for Dermoptera, Pholidota, and Tubulidentata, to name the three orders with the least amount of living diversity. That we do not merely relegate Galeopithecidae, Manidae, and Orycteropodidae to Eutheria incertae sedis has to do partly with taste and history, but also partly with a persistent desire that classification reflect phenetic distance as well as phylogeny. For example, keeping rodents and lagomorphs as distinct orders continues to make good sense, because the skein of morphological—and now also molecular—evidence concerning their alleged sister-group relationship remains as tangled as ever (but for a more optimistic view, see Novacek et al., 1988). *Plesiorcyteropus* is a highly derived form that cannot be placed within the confines of any eutherian order as currently defined. For this reason, plus the additional one that it would be systematically untidy to leave a Recent mammal incertae sedis as to order, a new ordinal level taxon is warranted.

3. *Plesiorcyteropus* is still not completely known osteologically, and with the discovery of new material its appropriate placement within some existing order will become clear.

It is reasonable to believe that additional fossils of *Plesiorcyteropus* will be discovered in future, in view of the very active programs of subfossil recovery now being undertaken in Madagascar. But there are actually very few important gaps left in our basic knowledge of the bibymalagasy skeleton, and what

we have already shows us that its skeletal bauplan does not accord closely with that of any other major eutherian taxon. The few postcranial bones that are as yet unknown, such as those of the hands and feet, are unlikely to provide much insight about relationships—but are very likely to exhibit the same pervasive adaptations for digging seen elsewhere in the skeleton. Whatever the shape of these adaptations may turn out to be, it is sure that they will be paralleled in more than one possible relative. As for the skull, the only parts that are completely unknown are concerned with the masticatory apparatus. I agree that this particular gap in knowledge is important, but filling it will not necessarily lead to resolution of the basic systematic problem. While I believe Patterson (1975) was probably right in inferring that *Plesiorcyteropus* was edentulous, this is not yet known for a verifiable fact and therefore cannot be part of any diagnosis. If it is eventually demonstrated that *Plesiorcyteropus* possessed at least *some* teeth, certain now-contentious points may be resolved. I accept that teeth composed of tubulodentine would be definitive for the tubulidentate hypothesis, my contrary interpretation of the cranial and postcranial evidence notwithstanding. Enamelless teeth might favor a broad if still uncertain xenarthran connection. Teeth of more normal eutherian aspect may or may not be dispositive: everything would hinge on what, if anything, they might resemble. In the meantime, *Plesiorcyteropus*—and therewith Bibymalagasia—must be defined on a medley of cranoskeletal features that clearly set this taxon apart from every other, but just as clearly offer very little immediate help in resolving its affinities. In short, while it is to be hoped that knowledge of *Plesiorcyteropus* will increase, there may be no corresponding improvement in what we can do with it. Even so, submergence of *Plesiorcyteropus* in some currently defined eutherian order is unlikely to be defensible below the level of suborder, for which Bibymalagasia would remain a suitable nomen.

4. The character list used for the parsimony analysis is defective because it includes too many characters affected by homoplasy.

This point is probably correct, but I do not see what can be done about it. Many more

characters could be added to the list I defined; however, I believe that the only practical result of doing so would be to further decrease the stability of higher-level associations and therewith the confidence with which the results can be viewed. An alternative, here considered objectionable, is to proceed in the same way that Patterson (1975) did, and assert that certain characters (and taxa) can be excluded from study or comparison solely on the basis of private knowledge about homology and relationships. It would be hypocritical to argue that I have not also made exclusions, based on my assessment of preliminary data. However, I have attempted to detail for the reader where and why such exclusions have been made.

In closing, I find it necessary to point out that the function of a program like PAUP is not to find the "right" answer to a particular systematic problem, but merely to identify the least defective. Relative defectiveness is adjudicated by application of a parsimony criterion, usually associated with William of Ockham, that in slicing the world into categories, one shall not multiply entities needlessly—nor, by extension, steps in a cladogram. In modern systematics, the least defective cladogram is understood to be the one with the greatest stability, which in turn is usually considered to be the one with the

least amount of remanent, unexplained similarity that must be due to homoplasy. But when multiple possible solutions are found that are seemingly equipotential, which, if any, is to be regarded as "best?" As Popper (1972) himself noted, parsimony is not a test that permits one to choose decisively among alternatives on the basis of their ability to withstand falsification. It is instead an ad hoc device that permits one to make a selection among *such competing alternatives as are known to exist*. Parsimony does not help you "discover" anything, except the limits of what you are willing to accept. When different researchers using different data sets converge on the same or similar solutions for a particular systematic problem, we call such results "robust," to differentiate them from others in which the nimbus of uncertainty continues to mask whatever signal the data may in fact contain. In the present case, there are several possible solutions for the sister group of *Plesiorcyteropus*, none of which is judged to be convincing. My solution is therefore to state that there is no solution, except to recognize that *Plesiorcyteropus* cannot be securely placed within an existing order and must be set apart on the eutherian cladogram. This is not an antiparsimonious result, because sometimes it really is needful to multiply entities. Ockham's razor cuts both ways.

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APPENDIX 1: IS *LEPTOMANIS* A RELATIVE OF *PLESIORYCTEROPUS*?

Isolated bones of reputed manid or orycteropodid affinity have been recovered at several Palaeogene localities in western Europe. I have not seen any of the original material and therefore have little to add to accounts by Simpson (1931), Emry (1970), Koenigswald (1969), and Storch (1978). However, a few comments are warranted on the holotype of *Leptomanis edwardsi* (MNHP Qu 11180), which, according to Thewissen (1985), displays several substantive resemblances to *Plesiorycteropus*.

The holotype of *Leptomanis edwardsi* is a calvarium in poor condition from Larnagol, France (Filhol, 1894). Filhol (1894) regarded *L. edwardsi* as a probable manid, although other tentative allocations have also been suggested (Dasypoidea, by Ameghino [1905] and ?Orycteropodidae by Simpson [1931]). Since Emry's (1970) study, the balance of opinion has shifted back to Filhol's original interpretation. In particular, Storch (1978) has argued that *L. edwardsi* is in fact a synonym of *Necromanis quercyi*, a taxon based on a

manidlike humerus from France (Filhol, 1894). This allocation, if correct, provides additional support for Koenigswald's (1969) contention that virtually all known manid remains from Late Eocene/Early Oligocene localities in Western Europe can be allocated to species of a single genus, *Necromanis*.

Contrary to this trend, Thewissen (1985) regarded *Leptomanis* as a tubulidentate rather than a manid. His character analysis is limited to comparisons to manids and orycteropodids (within which he included *Plesiorhycteropus*). He did not consider Storch's (1978) evidence for including *Leptomanis* within *Necromanis*. The following list consists of Thewissen's character states for *Leptomanis* (in italics), together with my independent assessment of conditions in *Plesiorhycteropus*.

(1) *Nasals rostrally broadened*. Thewissen (1985: 277) stated that the nasals of *Leptomanis* "resemble those of *Plesiorhycteropus* [but not *Orycteropus*]. . . in that they broaden rostrally." Published photographs of the *Leptomanis* calvarium (e.g., Guth, 1958: fig. 2A) indicate that the degree of broadening is rather restrained by comparison to that of *Plesiorhycteropus*.

(2) *Lateral part of nasofrontal suture medially directed*. This character may be restated to read that the angle formed between the internasal suture and the nasofrontal suture is less acute in orycteropodids than in manids. Manids, however, are variable. In *Manis javanica* and *M. gigantea*, the nasals are posteriorly narrow and deeply wedged into the frontal. In *M. tetradactyla*, by contrast, the nasals are considerably wider caudad, and the internasal/nasofrontal suture angle is about the same as in orycteropodids. To the degree that any difference in character states is meaningful, *Leptomanis* is like *Orycteropus* and *M. tetradactyla*, while *Plesiorhycteropus* apparently resembles the majority of manids in having a more acute angle.

(3) *Antorbital suture steep*. *Leptomanis* is said to be more like manids than *Orycteropus* in the steepness of the sutural contact between the frontal and the maxillary; *Plesiorhycteropus* is like orycteropodids. I find that the contrast in conditions is rather slight.

(4) *Postorbital process a low, blunt ridge*. The condition in *Leptomanis* is decidedly dif-

ferent from that of *Orycteropus*, in which the postorbital process is a well-developed, projecting prong. Thewissen noted that MNHN 327 (now the holotype of *P. germainepetterae*) possesses a low ridge (my temporal tubercle) in the same place. The other skulls (representing *P. madagascariensis*) do not, which may be taken as a minor species difference. I agree with Storch (1978) that the orbital rim of *Leptomanis* resembles that of *Manis*.

(5) *Four frontal emissary foramina*. The existence of several foramina in *Leptomanis* is apparently to be taken as an autapomorphy, since none of the compared taxa has as many.

(6) *Squamosal dorsally extensive and frontosquamosal suture long*. This represents another remarkable apomorphy of *Leptomanis*. If Thewissen's figure 5 is correctly drawn, the squamosal extended onto the dorsal aspect of the skull to a degree not found in any other mammal (with the possible exception of didymoconids; Meng Jin, personal commun.), in a configuration that left very little room for the parietals. As a result no meaningful comparisons can be made to other taxa, inasmuch as they lack or express only negligible frontosquamosal contact. It should be noted, however, that Storch (1978) interpreted the "frontosquamosal" suture as "frontoparietal."

(7) *Zygomatic process of the squamosal projects laterally*. The contrast here is with manids, in which the process projects ventrally. But in almost all other mammals, this process projects laterally, so the resemblance to orycteropodids and *Plesiorhycteropus* is not noteworthy. Storch (1978) did not discuss the position of the zygomatic process of the squamosal, probably because little more than its root remains.

(8) *Orbitosphenoid large*. The orbitosphenoid is large in *Plesiorhycteropus*, but that of *Orycteropus* is larger still, extending well above the level of the ethmoid foramen. This also seems to be true of *Leptomanis*, assuming that the ethmoid foramen is correctly identified (see next character).

(9) *Ethmoid foramen situated on frontal-orbitosphenoid suture*. This is the position found in orycteropodids and *Plesiorhycteropus*, but not in manids (which have a small

orbitosphenoid). It should be noted that Thewissen's identification of this foramen is tentative, since the relevant area is broken in the *Leptomanis* skull. The position of the foramen is unusual in that it is situated rostroventral to the optic canal, whereas in orycteropodids and *Plesiorycteropus* (and most other mammals that express this feature) it is situated rostradorsal to the canal.

(10) *Cranio-orbital foramen (of sinus canal) present.* This feature is present in *Orycteropus*, *Plesiorycteropus*, and manids (but see Morphology of the Cranium).

A few other traits of *Leptomanis* are mentioned but are not described in enough detail to permit comparisons. Thewissen concluded that, overall, *Leptomanis* is more like orycteropodids than manids except for features connected with the sutural boundaries of the frontal. Counted as special resemblances to *Orycteropus* are the lateral position of the root of the zygomatic process of the squamosal and the dorsal extension of the orbitosphenoid.

My assessment of the evidence is rather different. I find that the cited special resemblances of *Leptomanis* and *Orycteropus* are frequently encountered in other mammals (e.g., lipotyphlans) and therefore provide no basis for exclusive brigading of these two taxa. Most of the rest of the noted resemblances are also widely distributed (e.g., presence of the cranio-orbital foramen). It is of some interest that, for a few traits, *Leptomanis* is distinctly more like *Plesiorycteropus* than either manids or *Orycteropus*.

The apparent dorsal extension of the squamosal in *Leptomanis* and the position of the ethmoid foramen vis-à-vis the optic canal are peculiar, and further study is needed to in-

terpret these conditions. It is also odd that the orbitosphenoid has a lengthy direct contact with the squamosal that is not broken by an intervening tongue of the alisphenoid, and that the root of the zygomatic arch is situated at the extreme anterior end of the squamosal rather than more posteriorly. These are very unusual conditions (although they are nearly replicated in manids) and are completely absent in orycteropodids and *Plesiorycteropus*. On the other hand, these relations would appear less bizarre if most of the bone identified as squamosal is actually parietal—in which case one would have to infer complete obliteration of the parieto-squamosal suture.

In any event, it is clear that the *Leptomanis* skull is far too imperfectly preserved to bear much further analysis. So far as it is possible to interpret this cranium, the pholidotan hypothesis of Storch (1978) seems slightly more supportable than the tubulidentate one of Thewissen (1985). However, I question whether Storch's evidence is sufficient to sink *Leptomanis edwardsi* into *Necromanis quercyi*, in view of the former's substantial departures in cranial construction from any known pholidotan model. Some of these departures represent morphological approaches to *Plesiorycteropus*, but none of them is compelling enough to warrant a conclusion of real relationship.

The postcranial remains of diverse nominal species of Tertiary manids that Koenigswald (1969) placed in *Necromanis* do not require special comment. As both he and Emry (1970) showed, they are definitely manid; and, like the postcrania of extant manids, they display few important resemblances to conditions encountered in bibymalagasy.

